Decision support for seascape conservation and ecosystem-based marine management in the northern Baltic Sea

ELINA VIRTANEN

ACADEMIC DISSERTATION
To be presented, with the permission of the Faculty of Science
of the University of Helsinki, for public examination in banquet room 303,
Unioninkatu 33, on 19th of October 2020, at 12 o´clock.

DEPARTMENT OF GEOSCIENCES AND GEOGRAPHY A87 / HELSINKI 2020

Cover photo: Juuso Haapaniemi

Author´s address: Elina Virtanen
Marine Research Centre
Finnish Environment Institute
Latokartanonkaari 11
00790 Helsinki, Finland

Supervised by: Research Director Atte Moilanen
Department of Geosciences and Geography
University of Helsinki

Reviewed by: Professor Erik Bonsdorff
Environmental and Marine Biology
Faculty of Science and Engineering
Åbo Akademi University

Senior research scientist Matt White
Biodiversity Division, Department of Environment, Land,
Water & Planning
Arthur Rylah Institute for Environmental Research, Australia

Opponent: Professor Mary Wisz
Section for Ocean Sustainability, Governance and Management
World Maritime University
Senior scientist at National Institute of Aquatic Resources
Section for Ecosystem-Based Marine Management
Technical University of Denmark

ISSN-L 1798-7911
ISSN 1798-7911 (print)
ISBN 978-951-51-6576-3 (paperback)
ISBN 978-951-51-6577-0 (pdf)
http://ethesis.helsinki.fi

Unigrafia Oy, Helsinki 2020

"No blue, no green."
Sylvia Earle

Virtanen E., 2020. *Decision Support for Seascape Conservation and Ecosystem-Based Marine Management in the Northern Baltic Sea*. University of Helsinki, Department of Geosciences and Geography A87. Unigrafia Oy, Helsinki. 54 pages, 4 figures and 2 tables.

Abstract

Marine ecosystems are degrading around the world at an unprecedented rate. Loss of biodiversity, population declines, invasion of non-indigenous species, and change in community composition are apparent in all marine ecosystems. Various policies at multiple management levels address these challenges with specific targets for good ecological and environmental status of marine areas. While various policies, directives and strategies are applicable at global and regional levels, threats facing marine ecosystems in coastal areas are more localized. Thus, to achieve effective results, conservation and management actions should be designed and addressed locally, and carefully targeted to maximize cost-efficiency and benefits for the marine ecosystem.

In this thesis, four case studies are developed which demonstrate how spatially explicit analyses can support seascape conservation, sustainable use of marine areas, as well as effective management actions: (1) locate key areas for conservation, (2) pinpoint areas for effective nutrient abatement, (3) identify locations for marine mineral extraction, and (4) estimate potential future changes in key communities with the projected declines in marine environment. This thesis aims to show how extensive data combined with appropriate spatial analysis paths together with cross-discplinary marine science can support seascape conservation and ecosystem-based marine management. The role of management in sustaining marine biodiversity is investigated and the applicability of methods developed in terrestrial realm to marine environments is evaluated.

The case studies are located in the northern Baltic Sea, where multiple stressors threaten marine biodiversity. The work relies on extensive species inventory data from 140,000 underwater sites, collected by the Finnish Inventory Programme for the Underwater Marine Environment (VELMU). Statistical modelling was used in case studies (1) and (4) to explain the distribution of species, and further in case studies (2) and (3) in describing hypoxia probabilities and the occurrence of ferromanganese concretions, respectively. Further, key areas for conservation were identified with spatial prioritization in case study (1).

Based on the results, current marine protected areas (MPAs) leave almost three-quarters of ecologically important species occurrence areas unprotected. This highlights the need to further develop current MPA network, and the role of spatial planning in guiding the allocation of marine areas to human activities. Knowledge of unprotected key areas can be further utilized to promote private seascape conservation and sustainable use of marine areas. In case study (2), areas naturally prone to hypoxia development were identified with spatial analyses, borrowing concepts and methodologies from landscape ecology. The approach developed can be used to optimally target nutrient abatement measures to where they are most likely to be efficient, as well as explain why some areas are more or less immune to nutrient abatement actions already taken. Case study (4) further emphasizes that some areas would benefit more from nutrient abatement measures than others. Case study (3) demonstrated that marine minerals, namely ferromanganese concretions, are more widespread than previously anticipated. As concretions hold high quantities of minerals targeted by the emerging seabed mining industry, there may be economic opportunities for such extraction activities to take place also in the Baltic Sea. Results of case studies (1) and (3) can guide detrimental mining activities to ecologically less valuable areas, where abundant concretions can be found.

Spatially explicit analyses described in case studies (1)–(4) can provide valuable support for seascape conservation and ecosystem-based management and can give further guidance for sustainable use of marine areas. Finally, efficient management of marine areas requires the integration of local management actions into wider policy processes. Ecosystem-based marine spatial planning needs to adopt place-based management strategies and decisions that are actionable at various spatial scales and can be implemented locally.

Keywords: ecosystem-based management, spatial prioritization, statistical modelling, species distribution modelling (SDM), seascape ecology, Marine Protected Areas (MPAs), systematic conservation planning (SCP), hypoxia, ferromanganese concretions

Tiivistelmä

Meriekosysteemien tila heikkenee kiihtyvällä tahdilla ympäri maailman. Jo nyt kaikissa maailman merissä monimuotoisuus hupenee, populaatiot pienenevät, vieraslajit leviävät ja lajien yhteisörakenteessa tapahtuu muutoksia. Näitä haasteita ratkotaan monella eri poliittisella tasolla, ja meren hyvälle ekologiselle tilalle pyritään asettamaan selkeitä tavoitteita. Monet direktiivit, säädökset ja linjaukset ovat globaaleja ja alueellisia, vaikka meriekosysteemejä kohtaavat uhat, erityisesti rannikolla, ovat hyvin paikallisia. Parhaiden tulosten saavuttamiseksi direktiivien ja säädösten toimeenpanon pitäisi olla paikallisesti suunniteltuja ja huolellisesti kohdennettuja siten, että merien käytön kustannustehokkuus ja meriekosysteemien säilyvyys voitaisiin turvata.

Tässä väitöskirjassa osoitetaan neljän tapaustutkimuksen keinoin, miten paikallisesti räätälöidyt spatiaaliset analyysit voivat tukea tehokasta meren suojelua ja hallintaa: (1) paikallistamalla suojelun avainalueet, (2) osoittamalla alueet tehokkaalle ravinteiden vähentämiselle, (3) tunnistamalla kohteet mereisten mineraalien louhinnalle ja (4) arvioimalla mahdolliset muutokset avainyhteisöissä heikkenevän meren tilan myötä. Tämä väitöskirja osoittaa, miten laajat aineistot ja spatiaaliset analyysit yhdessä poikkitieteellisen merentutkimuksen kanssa voivat tukea meren suojelua ja ekosysteemilähtöistä meren käytön hallintaa, ja mikä rooli merien käytön suunnittelulla on meren monimuotoisuuden ylläpitämisessä. Väitöskirjan tavoitteena on myös arvioida alun perin terrestriselle puolelle kehitettyjen työkalujen käytettävyyttä meriympäristössä.

Tapaustutkimukset sijoittuvat pohjoiselle Itämerelle, jossa meriympäristössä kertaantuvat paineet uhkaavat meriluonnon monimuotoisuutta. Tutkimukset nojaavat laajaan vedenalaiseen inventointiaineistoon 140,000 näytepisteeltä, jotka on kerätty Suomen vedenalaisen meriluonnon monimuotoisuuden inventointiohjelmassa (VELMU). Tilastollista mallinnusta käytettiin tapaustutkimuksissa (1) ja (4), joissa mallinnettiin lajien levinneisyyttä, ja edelleen tapaustutkimuksissa (2) ja (3), joissa kuvattiin vastaavasti hapettomuuden todennäköisyyksiä ja mereisten mineraalien, rautamangaanisaostumien esiintymistä. Lisäksi tapaustutkimuksessa (1) tunnistettiin suojelulle tärkeitä alueita spatiaalisen suojelupriorisoinnin avulla.

Tulosten perusteella nykyiset merisuojelualueet jättävät melkein kolme neljäsosaa ekologisesti merkittävien lajien esiintymisalueista suojelematta. Tämä korostaa tarvetta kehittää edelleen nykyistä merensuojelualueiden verkostoa sekä aluesuunnittelun roolia toimintojen sijoittelussa merialueilla. Suojelematta jääneitä alueita voidaan suositella suojeltavaksi yksityisillä suojelualueilla ja ottaa huomioon meren kestävässä käytössä. Toisessa tapaustutkimuksessa tunnistettiin luonnollisesti hapettomia alueita, lainaten käsitteitä ja menetelmiä maisemaekologiasta. Tällä lähestymistavalla voidaan kohdentaa toimenpiteitä ravinteiden vähentämiseen alueille, joista niistä on eniten hyötyä, ja toisaalta selittää miksi jotkin alueet ovat immuuneja jo tehdyille vähentämistoimenpiteille. Neljännessä

tapaustutkimuksessa myös esitettiin, miten eri alueet reagoivat eri tavoin ravinteiden vähentämiseen johtaviin toimenpiteisiin. Kolmannessa tapaustutkimuksessa havainnollistettiin, miten mereiset mineraalit, tässä esimerkkinä rautamangaanisaostumat, ovat huomattavasti laajemmalle levinneitä kuin aiemmin on luultu. Koska saostumat sisältävät suuria määriä kaivosalan tavoittelemia mineraaleja, mereiselle kaivostoiminnalle saattaa olla tulevaisuudessa taloudellisia edellytyksiä Itämerellä. Tapaustutkimukset (1) ja (3) voivat ohjata mereistä kaivostoimintaa ekologiselta kannalta vähiten arvokkaille alueille, ja toisaalta alueille, joilla saostumia esiintyy runsaasti.

Tapaustutkimukset 1–4 voivat tukea päätöksentekoa, jotka liittyvät meren suojeluun ja ekosysteemilähtöiseen meren kestävään käyttöön. Merialueiden käytön tehokas hallinta vaatii myös paikallistoimien integrointia laajempiin politiikkaprosesseihin. Ekosysteemilähtöisen merialuesuunnittelun pitää omaksua strategioita ja päätöksiä, jotka ovat toteutettavissa monella eri mittakaavan tasolla, ja joita voidaan soveltaa paikallisesti erilaisilla alueilla.

Asiasanat: ekosysteemilähestymistapa, meren käytön hallinta, spatiaalinen priorisointi, tilastollinen mallinnus, lajien levinneisyysmallinnus, merimaisemaekologia, merisuojelualueet, systemaattinen suojelusuunnittelu, hypoksia, rautamangaanisaostumat

Acknowledgements

First and foremost, I would like to thank my supervisor Atte Moilanen. As you Atte said it: always collaborate with people smarter than you, it will take you a long way. And indeed, it has. Thank you Atte for your consistent support, guidance, mentorship and encouragement throughout this dissertation (and beyond) and thank you for your friendship.

Secondly, I would like to express my sincere gratitude to all the people who have collected VELMU data for all these years, especially in Parks and Wildlife Finland. Without your field efforts this thesis would not exist. In addition, I would like to acknowledge the whole VELMU project group, and all the people who have been involved in the project, in some way or another, irrespective of institute in question, and especially Markku Viitasalo, Wilma Viljanmaa and Penina Blankett for the VELMU coordination.

I would like to thank my co-authors, particularly Make for your idealism, enthusiasm and optimism (even criticism), which have positively influenced the somewhat pessimistic side of me as a researcher. I would like to say a special thank you to Juho for your cool head, tenacious attitude towards data management, and your interest in model optimization – it truly was a pleasure to work with you. I wish to also thank Antonia for interesting science- and not-so-science-related conversations (e.g. in Pharmarium and thereabouts), Alf for delightful discussions regarding benthic fauna and hypoxia (4.6 is the answer to everything), Laura for your inspirational energy towards science and your excellence in color/graphics visualizations, Kirsi for your know-how in, well, almost everything, Ale for your expertise in marine geology, and lastly, Kari and Sofia for your collaboration in remote sensing. A huge, collective thanks goes also to various people in several institutes, whom I´ve had the pleasure to work with for the past few years.

I am also grateful to the pre-examiners of this thesis, Professor Erik Bonsdorff and senior research scientist Matt White, and to the thesis committee members, Tuuli Toivonen and Laura Uusitalo.

In addition, I would like to thank several colleagues in the SYKE Marine Research Centre for (non-)professional discussions, and especially colleagues in the MMK unit for your support and company. A special thanks, *asanteni*, goes to the "Six Degrees South" group – some moments to remember! A huge thanks goes also to the unofficial support groups, namely "Cat therapy", "Sister and her brother", "Gangs of Vaskio" and last, but not least, the shadow division of "Marine scientists above the water".

Lastly, I would like to acknowledge financial support from the Finnish Inventory Programme for the Underwater Marine Environment (VELMU), funded by the Ministry of the Environment and the SmartSea project (grants 292985 and 314225) funded by the Academy of Finland Strategic Research Council.

Contents

List of original publications

This thesis is based on the following publications:

I. Virtanen, E. A., M. Viitasalo, J. Lappalainen, and A. Moilanen (2018). Evaluation, gap analysis, and potential expansion of the Finnish marine protected area network, *Frontiers in Marine Science*, 5, 402, doi:10.3389/fmars.2018.00402.

II. Virtanen, E. A., A. Norkko, A. Nyström Sandman, and M. Viitasalo (2019). Identifying areas prone to coastal hypoxia – the role of topography. *Biogeosciences* 16, 3183–3195, doi:10.5194/bg-16-3183-2019.

III. Kaikkonen*, L., E. A. Virtanen*, K. Kostamo, J. Lappalainen, and A. T. Kotilainen (2019). Extensive coverage of marine mineral concretions revealed in shallow shelf sea areas. *Frontiers in Marine Science* 6, 541, doi:10.3389/fmars.2019.00541. *These authors contributed equally to this work

IV. Lappalainen, J., E. A. Virtanen, K. Kallio, S. Junttila, and M. Viitasalo (2019). Substrate limitation of a habitat-forming genus Fucus under different water clarity scenarios in the northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 218, 31–38, doi:10.1016/j.ecss.2018.11.010.

The publications will be referred to in the text by their roman numerals.

Author´s contribution

	I	II	III	IV
Original idea	EV, AM, MV	EV, MV	EV, LK, KK, AK	EV, MV, JL
Analyses	EV, JL, AM	EV, ANS	EV, LK	JL, EV, SJ, KYK
Manuscript preparation	EV, MV, JL, AM	EV, MV, ANS, AN	EV, LK, KK, AK, JL	JL, EV, MV, SJ, KYK

EV=Elina Virtanen, AM=Atte Moilanen, MV=Markku Viitasalo, JL=Juho Lappalainen, LK=Laura Kaikkonen, AN=Alf Norkko, ANS=Antonia Nyström Sandman, KK=Kirsi Kostamo, AK=Aarno Kotilainen, KYK=Kari Y. Kallio, SJ=Sofia Junttila

Abbreviations

BSAP	Baltic Sea Action Plan
BRT	Boosted Regression Trees
CBD	Convention on Biological Diversity
EBM	Ecosystem-Based Management
GES	Good Ecological Status (WFD)
GES	Good Environmental Status (MSFD)
HD	Habitats Directive
HELCOM	Baltic Marine Environment Protection Commission
IUCN	The International Union for Conservation of Nature
MPA	Marine Protected Area
MSFD	Marine Strategy Framework Directive
MSP	Marine Spatial Planning
MSPD	Maritime Spatial Planning Directive
SDM	Species Distribution Modelling
WFD	Water Framework Directive
Zeu	Euphotic depth

List of figures

List of tables

1 Introduction

Around the world, marine ecosystems are deteriorating at an unprecedented rate (Worm et al. 2006, Halpern et al. 2019). Loss of biodiversity, population declines, invasions of non-indigenous species, and changes in community composition are apparent in all marine ecosystems (Halpern et al. 2008, Halpern et al. 2019). Moreover, a changing marine environment rearranges food-webs and shifts distribution ranges of various species (Sunday et al. 2012, Rocha et al. 2015, Molinos et al. 2016). Direct and indirect causes for the degradation include (and are not limited to) fisheries exploitation (Jackson et al. 2001), physical habitat destruction/alteration (Lotze et al. 2006, Airoldi et al. 2008, van Denderen et al. 2019), pollution (Islam and Tanaka 2004), ocean acidification (Fabry et al. 2008), eutrophication (Crain et al. 2009, Reusch et al. 2018), hypoxia (Breitburg et al. 2018) and global warming (Harley et al. 2006, Poloczanska et al. 2016, Jonsson et al. 2018).

As the anthropogenic capacity to industrialize and economize the ocean grows, increasing human activities in the marine realm are posing severe threats to marine ecosystems (Halpern et al. 2019). Decline of land-based resources acts as the catalyst for commercial interests on marine materials, food and space (Lester et al. 2018, Nyström et al. 2019). Shallow, coastal areas are shaped by various human activities and recent technological advances have propelled the exploitation of even the most remote parts of the ocean (Ramirez-Llodra et al. 2011). Oceans have become a new economic frontier, and costly endeavours, such as mining of deep-sea minerals, are now not only feasible but also imminent (Dunn et al. 2018). Intact seascapes, or “marine wilderness” areas, are found only in less accessible areas, at high seas and extreme latitudes (Jones et al. 2018).

In order to control these ecologically harmful processes and to steer the use of marine resources in a sustainable way, necessary actions should be sought at global, regional and local levels to curb negative environmental trends in marine ecosystems.

1.1 Pathways to sustainable use of marine areas

Steps have already been taken at multiple levels of management to improve the status of the marine environment. The idea of sustainable use of marine areas – and in general marine management – is to protect and enhance marine biodiversity, and to ensure the delivery of ecosystem services for the benefit of the society (Elliott 2011). Good Ecological Status (GES) of marine waters supports the capacity to deliver ecosystem services, which translates directly to economic benefits (Nieminen et al. 2019).

In Europe, the management of aquatic environments is orchestrated by various directives. The cornerstone of conservation is the Habitat Directive (HD) (Directive 92/43/EEC), which aims to protect habitats (Annex I) and species (Annex II) that are either biogeographically unique or in danger of disappearing. Areas are designated under protection in the Natura 2000 network based on the listed habitats and species in annexes I and II (Evans 2012). The objective of the

Water Framework Directive (WFD) (Directive 2000/60/EC) is “good ecological status” of the European surface waters, calling for mitigation of eutrophication. The Marine Strategy Framework Directive (MSFD) aims to achieve Good Environmental Status (GES) of the EU´s marine waters by 2020 (Directive 2008/56/EC). MSFD is also the first legislative instrument that ensures the protection of marine biodiversity in its entirety (MSFD 2012). The overall goal is to maintain marine biodiversity, regulate human activities and to ensure the sustainable use of marine areas. On a regional level, the Baltic Sea Action Plan (BSAP) integrates diverse management measures to restore the good ecological status of the marine environment by 2021, set by a regional sea convention, the Baltic Marine Environment Protection Commission (HELCOM) (HELCOM 2007). Although the HELCOM BSAP goals are broader, the ecological objectives are similar to MSFD descriptors, and thus can support the corresponding environmental actions of MSFD (de Grunt et al. 2018). In 2014, EU adopted the Maritime Spatial Planning Directive (MSPD) (Directive 2014/89/EU), designed to support the implementation of MSFD, and urged the member states to develop transparent marine spatial plans by the end of 2021 (MSPD 2014).

However, these nature, water and marine directives have not been successful in halting the declining trend of the state of marine ecosystems (EEA 2015). One reason is that the water and nature directives do not target the structure and functioning of the whole marine ecosystem or overall biodiversity. For instance, the WFD considers only certain indicator species for determining GES, and lacks holistic ecosystem indicators, and HD focuses on certain species and habitats only, which do not necessarily indicate a well functioning marine ecosystem (Moss 2008, Voulvoulis et al. 2017). A framework that considers ecosystems in a holistic way and integrates ecological and socio-economic objectives into management is needed (Rouillard et al. 2018).

Implementation of environmental and water policies has been promoted with the concept of Ecosystem-based Management (EBM) (or ecosystem approach to management). There is no single definition of EBM, but it constitutes of policies and management actions aiming to restore and enhance ecosystem health and resilience, and to conserve biodiversity, while at the same time delivering the services, goods and benefits required by the society (Atkins et al. 2011, Rouillard et al. 2018). EBM does not just strive to define management strategies for certain components of the ecosystem, but for the entire ecosystem.

Claims on marine space – driven by the need for food, materials, resources or infrastructure – require clear spatial visions on how activities should be distributed in order to maintain and manage marine ecosystems. Marine Spatial Planning (MSP) is a process where overlapping interests of different stakeholders are coordinated and tied together to make well informed decisions for the sustainable use of marine resources and conservation of marine biodiversity. MSP integrates in a holistic manner marine governance instruments related to the use of sea space from various sectors (Douvere 2008, Ehler 2009). While it is generally accepted that EBM needs to be integrated to MSP in order to achieve both ecological and socio-economic objectives, various environmental problems are still being tackled separately (Elmgren et al. 2015), and decisions about the allocation of marine space are based on single-sector objectives (Douvere 2008). Bringing all sectors together, EBM-MSP can form a mechanism for cross-sectoral collaboration, integrating conflicting requirements of various stakeholders, without jeopardizing the protection and condition of marine ecosystems (Bigagli 2015, Jones et al. 2016).

1.2 The Baltic Sea – multiple pressures

The Baltic Sea is a semi-enclosed, shallow coastal sea with steep vertical and horizontal environmental gradients. The basin is young from the geological and ecological perspective, and post-glacical processes are still undergoing (Leppäranta and Myrberg 2009, Snoeijs-Leijonmalm et al. 2017).

The Baltic Sea hosts a relatively small variety of species of marine and freshwater origin, of which only a few are endemic (Bonsdorff 2006, Ojaveer et al. 2010). Currently, the Baltic Sea suffers from eutrophication and increasing anthropogenic disturbance (Vahtera et al. 2007, Conley et al. 2011, Korpinen et al. 2012, Sundblad and Bergström 2014, Andersen et al. 2015, Andersen et al. 2017). Hypoxia is also one of the well-known problems of the Baltic Sea, occurring in central deep basins and in coastal zones, enhanced by the recent pace of excess anthropogenic nutrient loading (Conley et al. 2002, Conley et al. 2011, Jokinen et al. 2018).

In addition, the Baltic Sea is impacted by various anthropogenic activities, such as infrastructure development, commercial fishing and maritime traffic, which can lead to marked changes in species richness and community composition (Korpinen et al. 2012, Sundblad and Bergström 2014, Sagerman et al. 2020). Interests of economic sectors are also on the rise related to, for instance, marine mineral resource extraction, which can have negative impacts on marine ecosystems, especially in shallow water environments (Kaikkonen et al. 2018).

The Baltic Sea has also experienced offshore and coastal ecosystem-level changes, the disappearance of top predators and macrophytes, and altered foodwebs, driven by detrimental human activities, such as overfishing and coastal eutrophication (Torn et al. 2006, Österblom et al. 2007, Casini et al. 2008, Moksnes et al. 2008, Eriksson et al. 2011). Moreover, rapid colonization, invasion, and expansion by non-indigenous species has altered the ecosystem function and composition (Norkko et al. 2012, Jormalainen et al. 2016, Kotta et al. 2016).

Projected environmental changes further imply declining salinity levels, warming, and a worsening eutrophication status (Meier et al. 2011a, Meier et al. 2011b, Meier et al. 2012a, Meier et al. 2014). Such drastic changes, if realized, will have profound effects on the distributions of various species, which already live at the limits of their environmental tolerance (Vuorinen et al. 2015, Takolander et al. 2017a, Jonsson et al. 2018, Kotta et al. 2019). Although large uncertainties in such projections remain, rigorous adoption of BSAP measures would lead to improved environmental status of the Baltic Sea, despite the negative effects of climate change (Meier et al. 2018, Saraiva et al. 2019, Wåhlström et al. 2020). Together the history and future place the Baltic Sea under multiple threats, with cascading and interacting effects on marine ecosystem (Korpinen et al. 2012, BACC 2015). This challenge requires cross-border management strategies, as well as integrative, local management actions.

1.3 Seascape conservation and ecosystem-based marine management

Various policies and directives are operated and implemented at the regional level, with, for instance, targets set for the entire Baltic Sea, or for individual basins, such as the Baltic Proper or the Gulf of Finland. However, problems may be more localized in many coastal sea areas: for example nutrient discharges can sometimes be traced to a certain point-source (HELCOM 2018a), sediment loads can be linked to a certain dredging site (Bolam et al. 2006, Fettweis et al. 2011), and resuspension from recreational boating can impact a single bay (Sagerman et al. 2020).

To reach effective and cost-efficient outcomes, implementation should be carefully targeted at the local level to maximize benefits for the marine ecosystem. The extent of management actions required depends on the scale of activities and processes causing problems for marine ecosystems, as well as on the physical complexity of the area in question. Thus, management measures should be tailored and optimized to effectively tackle local challenges, and spatially explicit solutions should be sought to reach the goals of different policies that aim to mitigate anthropogenic pressures.

In this thesis, four case studies are developed which demonstrate how spatially explicit analyses can support seascape conservation and effective management actions. Motivations, challenges addressed, and solutions suggested in the case studies are briefly explained below.

1.3.1 Context of case study 1: Locate key areas for conservation

A key aspect in safeguarding marine biodiversity is the designation of Marine Protected Areas (MPAs). MPAs contribute to EBM and are perceived as an optimal way to safeguard marine biodiversity (Lester and Halpern 2008, Edgar et al. 2014). Especially no-take reserves have proven to support marine biodiversity and ecosystem functionality (Halpern and Warner 2002, Lester et al. 2009, Halpern 2014). The design of MPAs must be ecologically efficient to ensure the implementation of various conservation objectives, set by international policies (Edgar et al. 2014).

International and regional agreements require nations to designate areas under protection, and for instance the Natura 2000 network aims to protect key habitats and threatened species. The MSFD also states that marine biodiversity should be protected and maintained (MSFD 2012). In 2010, Convention on Biological Diversity (CBD) adopted a strategic plan to safeguard biodiversity, known as the Aichi target, which stated that: "*By 2020, at least 17% of terrestrial and inland water and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved* *through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures (OECMs) and integrated into the wider landscape and seascape*" (CBD 2010).

Conservation should thus be implemented through a network of ecologically coherent, well-managed and connected MPAs, and designated areas should be qualitatively and quantitatively adequate and representative (CBD 2010, HELCOM 2010, 2016). The post-2020 Global Biodiversity Framework by CBD is expected to scale up conservation efforts, and call for (up to) 30 % protection of land and sea areas by 2030, as it is evident that the conservation goals set in 2010 will not be reached by 2020 (EEA 2020).

Having a functioning network of MPAs presupposes that key areas are conserved. However, designation of MPAs is not necessarily based on site-specific knowledge of habitats and species, and can rely on *ad hoc* decisions (Agardy et al. 2011). Furthermore, conserving only certain habitats or individual species at the expense of overall marine biodiversity does not guarantee the long-term persistence or stability of ecosystems (Stevens and Connolly 2004, Jackson and Lundquist 2016). Unfortunately, data of sufficient breadth and quality for competent evaluation of the success of MPAs has been largely missing, and consequently analysis paths for MPA evaluation have been variable.

Suitable tools combined with solid data can enable the estimation of the ecological coherence of MPA networks and the identification of gaps in protection. Moreover, key areas for conservation outside the current MPAs could be identified to well-informed expansion, to reach ambitious goals of, for instance, CBD post-2020 biodiversity strategy (EEA 2020).

1.3.2 Context of case study 2: Indicate areas for effective nutrient abatement

The main goal of MSFD has been the GES of marine waters by 2020, which, based on the current knowledge (e.g. Korpinen et al. 2018), will not be reached. One of the main targets of MSFD in the Baltic Sea and the HELCOM BSAP has been the reduction of eutrophication and resulting hypoxia.

Biogeochemical processes contributing to hypoxia formation are well-known and are often associated with high anthropogenic nutrient loading and high primary productivity as well as strong temperature or salinity stratification (Bonsdorff et al. 1997, Conley et al. 2011). Nutrient loading and hypoxia are connected through internal loading of nutrients from anoxic sediment, creating a vicious circle of eutrophication (Vahtera et al. 2007). Moreover, physical conditions, such as complexity of coastal areas or heterogenous archipelago limiting lateral movement of water, often create opportunity for hypoxia to develop (Conley et al. 2009, Rabalais et al. 2010, Breitburg et al. 2018, Fennel and Testa 2019). Ecological consequences of lack of oxygen vary from dysfunctioning benthic communities to mass mortality of benthic animals (Vaquer-Sunyer and Duarte 2008, Norkko et al. 2015, Gammal et al. 2017).

However, challenges remain in projecting spatial and temporal variability of hypoxia in coastal environments.

Hydrodynamic-biogeochemical models have mostly been developed for the entire Baltic Sea (Eilola et al. 2009, Neumann 2010, Meier et al. 2011a, Meier et al. 2012a). While these models are useful at regional and basin scales, their horizontal resolution (usually 2 to 3 nautical miles) is too coarse for guiding effective, local management actions in coastal areas, especially within archipelago.

Finding alternative ways to pinpoint areas prone to coastal hypoxia in coastal areas are necessary. If nutrient abatement measures could be directed cost-efficiently to areas most urgently needed – and avoided in areas naturally problematic where abatement measures most probably fail – environmental and economic benefits could be maximized.

1.3.3 Context of case study 3: Identify areas for marine mineral extraction

One of the aims of MSPD is to support "Blue Growth", i.e. sustainable economic growth and use of resources in the marine areas (MSPD 2014). As the pool of land-based resources drains, extraction of sea-floor materials becomes economically viable (Jouffray et al. 2020). The demand for raw materials is on the rise, and untapped mineral potential is of interest to the seabed mining industry (Hannington et al. 2017). For instance, mineral deposits hold large quantities of commercially exploitable metals, such as iron, manganese and cobalt (Kuhn et al. 2017).

The environmental impacts of seafloor mining can be substantial, and planning of mineral extraction needs to consider not only the actual locations of the resource, but also adjacent areas (Kaikkonen et al. 2018). Thus, in addition to locating the economically most profitable areas, it is imperative to identify areas that are ecologically sensitive to extraction activities. If extraction of marine resources is steered so that impacts on marine biodiversity become minimized while economic benefits are maintained, the sustainability of future resource utilization could be improved.

1.3.4 Context of case study 4: Consider expected change in key communities to adjust mitigation measures

Both MSFD and WFD call for improved status of marine waters and aim to control eutrophication. The role of MSPD is to support both directives to achieve their objectives (MSPD 2014). The goal of national marine spatial planning is to identify and evaluate the current needs for marine space, and a critical part of the MSP process is analyzing future conditions (Ehler 2009). With the projected environmental change in the marine environment, integration of the temporal dimension with spatial aspects would benefit planning.

Understanding the consequences of expected changes to future marine ecosystems is necessary, both for spatial conservation measures and mitigation of eutrophication. As habitat-forming species have an important role in ecosystem structure and functioning, assessing the impacts of environmental change on their spatial distributions is essential. Scenario-based methods are useful for assessing the effects and intensity of environmental changes, such as consequences of decresing salinity on species ranges (Jonsson et al. 2018).

Eutrophication is related to vertical

light availability in the water column, which in turn influences the maximum depth of plant growth. For instance, depth-penetration of *Fucus* spp., one of the most important keystone species in the Baltic Sea, has been used as a biological indicator for ecological status in WFD. Estimating how increasing turbidity limits occurrences of such habitat-forming species is essential for estimating how communities might adapt to mitigation measures, and to focus future management actions to optimal areas.

1.4 Support for seascape conservation and ecosystem-based marine management: spatial analyses

Seascape conservation and sustainable use of marine areas requires suitable tools, of which many fall under the realm of geographic data science. A key class of methods is statistical modelling, where models are used to explain the relationships between observations and background variables. From an ecological perspective, one useful framework is Species Distribution Modelling (SDM), which combines species observations with environmental characteristics. SDMs draw correlative conclusions about a species and its habitat (ecological niche) and use that information to predict species occurrence patterns across landscapes (or seascapes) (Elith and Leathwick 2009). The use of SDMs can be roughly categorized to: (1) explanation, (2) prediction and (3) projection. Explanative SDMs investigate the statistical relationship of species with its environment and develop hypotheses of the environmental factors that explain the distribution of the species. Predictive SDMs use the explanative species-environment models to identify potential distributions in present time and/or similar region, and projected SDMs extend the species-environment relationship to the future and/or novel geographies (Araújo et al. 2019).

In the terrestrial realm, the use of SDMs has proliferated for the past decades, and SDMs have been used to address a wide array of theoretical and applied questions, including conservation management (Guisan et al. 2013), climate change impacts (and adaptation) (Willis et al. 2015, Hällfors et al. 2016), and risk assessments (Jiménez-Valverde et al. 2011). However, the development of marine SDMs has lagged behind their terrestrial counterparts. There are various reasons for this, such as deficiencies in biological data collection, lack of information about environmental predictor variables, temporal mismatches between environmental and biological data, sampling biases, or insufficient resolution of hydrodynamic/biogeochemical surrogates (Robinson et al. 2011, Robinson et al. 2017). Moreover, process-based and monitoring studies have a long history in marine science, and small-scale and time series analyses have predominated, which has contributed to the lack of spatial data in the marine realm.

The development of geographic *marine* data science (marine GIS) is only now evolving, supported by novel marine mapping techniques (Brown et al. 2011), and rapid advances in understanding spatial patterns, gradients, scales and structures in the marine environment and seascape (Pittman 2017). Also, with the rise of MSFD and MSPD – and the economic, social and ecological analyses needed for their implementation – demand for georeferenced marine data has increased. This has further promoted the need to formulate a holistic, cross-disciplinary view of the whole marine ecosystem, where ecological and human dimensions become integrated, thereby supporting for instance, EBM-MSP.

Only for the last decade (or so) has there been a surge of spatially-explicit studies in the marine environment. Based on a recent review by Robinson et al. (2017), a large fraction of marine SDM applications have concentrated on conservation planning, assessing the impacts of climate change and spread of invasive species, or rather traditionally, modelling biogeographical ranges of marine species (Embling et al. 2010, Verbruggen et al. 2013, do Amaral et al. 2015, Weatherdon et al. 2016, Weinert et al. 2016). However, modelling is only the first step which needs to be taken before integrating knowledge into decisions.

Decision Support Tools (DSTs) have been developed to inform decision making and spatially explicit planning. DSTs can integrate large amounts of data, including the ecological and societal dimensions, contrast alternative planning options, and enable the evaluation of effectiveness of different management strategies. For instance, Integrated Valuation of Ecosystem Services and Tradeoffs, InVEST, quantifies ecosystem services produced under different scenarios (Sharp et al. 2018), the end-to-end ecosystem model Atlantis explores the full spectrum of processes that affect natural ecosystems, including oceanography, ecology, economy and society (Fulton et al. 2011), and the Cumulative Impact Assessment Tool evaluates the effects of human activities on ecosystem components (Halpern et al. 2008).

In terms of EBM and conservation planning, widely utilized tools include for instance Marxan (Ball et al. 2009) and Zonation (Moilanen et al. 2005), which are capable of identifying priority areas for protected area development. Zonation has also been used, e.g., in ecological impact avoidance and conflict resolution for renewable energy development (Santangeli et al. 2018), biodiversity offsets (Moilanen et al. 2020) and habitat restoration (Thomson et al. 2009). With the race to implement MSFD, there has been a corresponding rush in the development of DSTs specific for marine environments (Stelzenmüller et al. 2013, Pınarbaşı et al. 2017). However, a recent review concluded that tools are not widely utilized, with explanations varying from the complexity of DSTs to the lack of output details (Janßen et al. 2019). Various spatial methods – although commonly applied in the terrestrial realm – are not always easily adopted to the marine environment, as the transferability of such tools is largely dependent on the availability of suitable data.

1.5 Aims of this thesis

Seascape conservation and ecosystem-based management, also in terms of MSP, requires detailed information on ecological, societal and economic factors. One science-related impediment has been the lack of adequate georeferenced data (Martin and Hall-Arber 2008, Cornu et al. 2014). EBM-MSP is mostly about *what* type of activities can be regulated to occur *where* and *when.* As marine ecosystems, resources, and human activities are inherently place-based, all management decisions and strategies should be of spatial and temporal nature. Therefore, in order to maintain marine ecosystems in good condition a key question is where areas worth conserving are, and where anthropogenic activities – and mitigation measures – should be located.

This dissertation has multiple broad aims: (1) show how extensive data combined with suitable (spatial) analysis can support sustainable, ecosystem-based marine management; (2) highlight the intrinsic part sea governance plays in sustaining marine biodiversity; and (3) reaffirm the applicability and transferability of tools developed in the terrestrial realm to marine environments. More specifically, this dissertation seeks to find answers to:

- How to identify priority areas for conservation and sustainable sea governance? (**I-IV**)

- How to determine locations for cost-efficient nutrient abatement measures, maximizing the benefits for the marine environment (**II**)?

- How to recognize areas for the economic resource potential of marine minerals while at the same time avoiding impacts on biodiversity? (**I**, **III**)

- If management actions prove to be effective – or for some reason fail, how will alternative futures look like, from the perspective of marine biodiversity? (**IV**)

Contributions of studies to this thesis are as follows:

Paper I is the first comprehensive estimation of key marine biodiversity areas in Finland, and it synthetizes a large quantity of biological and anthropogenic information. The study tests the transferability of methods developed in terrestrial realm to marine realm with a large quantity of underwater data, shows an analysis path for *identifying priority areas for conservation*, evaluates the effectiveness of the current MPA network, and suggests optimal MPA expansion sites.

Paper II provides a novel way to predict and *identify areas prone to coastal hypoxia*, without data on currents, stratification, biological variables, or complex biogeochemical models. By borrowing concepts and methods from landscape ecology, this study quantifies the facilitating role seafloor complexity has in the formation of coastal hypoxia. The study provides a straightforward approach for identifying areas cost-effectively for nutrient abatement measures.

Paper III uses statistical modelling to *localize marine resources*, applied to the estimation of the distribution of ferromanganese concretions. The role of concretions in ecosystem functioning is still unknown, and as concretions hold high quantities of commercially exploitable metals, they are of great interest to the mining industry. This study contributes to the role sea governance has in impact avoidance, and to the steering of the economic usage of marine resources towards sustainability.

Paper IV Demonstrates with scenario modelling how *potential future changes* will affect key marine communities. This is demonstrated with increasing and diminish-hing water clarity scenarios, as water transparency is one of the most important factors that structure shallow water marine assemblages. How will functionally important keystone species, such as bladderwrack, *Fucus* spp., respond to changes in light availability, and thus to eutrophication?

2 Materials and methods

2.1 Study area

All four case studies are focused on the northern Baltic Sea, covering the territorial waters and exclusive economic zone of Finland. Case study **II** also covers the Stockholm archipelago (Figure 1).

The Finnish marine environment is characterized by strong environmental gradients of salinity, turbidity and exposure. Surface salinity ranges from 7 PSU in the southwestern, outer archipelago and reaches almost zero in the northernmost part of the Gulf of Bothnia, as well as near the river mouths, where freshwater enters the sea. Turbidity gradient follows similar patterns, as transport of dissolved and particulate organic matter from rivers and high on-site primary productivity elevates water turbidity and limits underwater light availability in the inner archipelago. In offshore, outer areas water clarity on average increases with lower primary productivity and higher water exchange between adjacent basins. Summertime cyanobacteria blooms may however at times decrease water transparency also in the offshore areas.

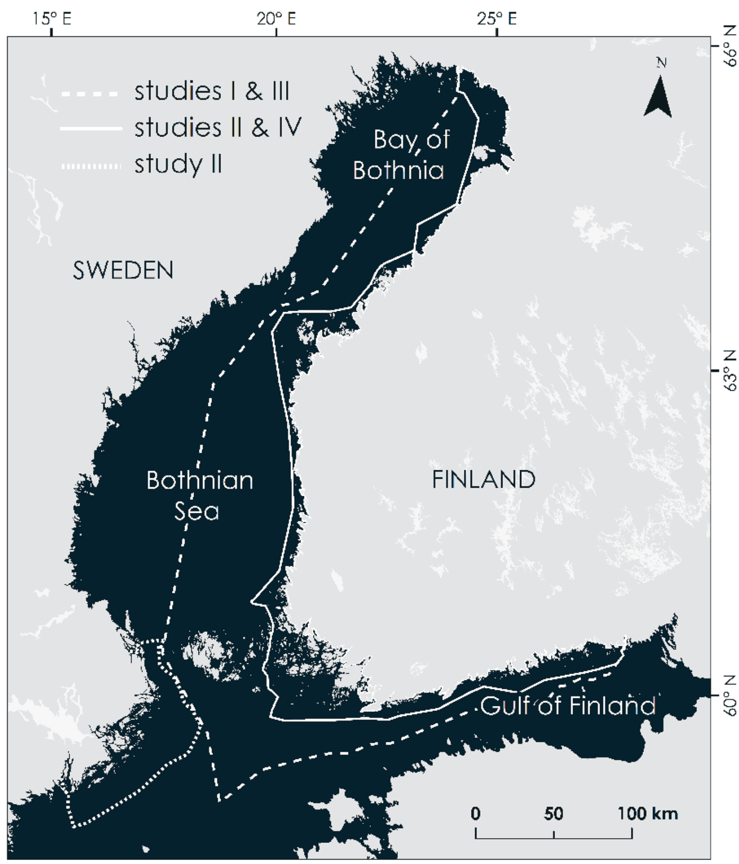

Figure 1. Case studies I–IV in the northern Baltic Sea.

Glacial erosion and deposition have formed the Finnish seabed to be geologically diverse and patchy, with a heterogeneous mixture of various substrate types. Glacial and post-glacial sediments consist mainly of till, clays, silts and fine-grained sediments. The crystalline bedrock can be characterized by tectonic lineaments and fracture zones, evident for instance in the Archipelago Sea, where deep, underwater "canyons" crisscross the seabed (Kaskela et al. 2012, Kaskela and Kotilainen 2017).

Finnish marine waters are rather shallow, with a mean depth of only 50 m, with the deepest parts (299 m) located southwest from Åland Islands. The most northern part, Bothnian Bay, is shallow and low-saline, with exposed shorelines and comparatively monotonic geomorphology. Moving south, the Kvarken in the middle of the Gulf of Bothnia acts as a biogeographical barrier between north and south. Continuing further south from the Kvarken, salinity levels increase, topography and geomorphology becomes more complex, and over 50,000 islands dot the Archipelago Sea (Viitasalo et al. 2017), creating one of the most complex archipelago systems in the world. The southern part, Gulf of Finland, resembles geomorphologically the Archipelago Sea, and is also heavily burdened with eutrophication, human-induced pressures, and hypoxia (Raateoja and Setälä 2016, Korpinen et al. 2018). Together this geomorphological and environmental complexity creates a variety of habitats for benthic organisms. Benthic communities are a mixture of species of freshwater and marine origin and are less diverse than "true" marine assemblages. In general, species richness, habitat and functional diversity in the Baltic Sea decrease from south to north, and are higher in shallow marine areas, compared to deep, dark seafloors (Bonsdorff and Pearson 1999, HELCOM 2012, Viitasalo et al. 2017).

2.2 Data

2.2.1 Data from below the surface

Studies **I**, **III** and **IV** utilize data from underwater inventories by the Finnish Inventory Programme for the Underwater Marine Environment, VELMU. Since 2004, VELMU has collected information on species, communities and habitats using mainly scientific diving and video observation methods. Visited sites range from enclosed, inner archipelago areas to exposed sites in the outer archipelago, as well as deep environments with soft seabed substrates. Inventories have been carried out mostly based on random stratified sampling, although some targeted inventories have followed fixed, systematic patterns, for instance for the purpose of delineating habitat types of Habitat Directive Annex I (Kaskela and Rinne 2018).

In 2019, ~160,000 sites had already been visited (Figure 2). Underwater videos form the bulk of the data; ~100,000 sites, explored with drop-video or remotely operated vehicle, 60,000 sites dived, and additional ~10,000 locations investigated with other methods (fish larvae sampling sites, benthos and geological sediment samples).

In the scientific diving method, a diver observes the coverage (%) of all macrophytes, sessile benthic invertebrates, and different bottom substrates along ~100 m long dive transects, every horizontal 10 m

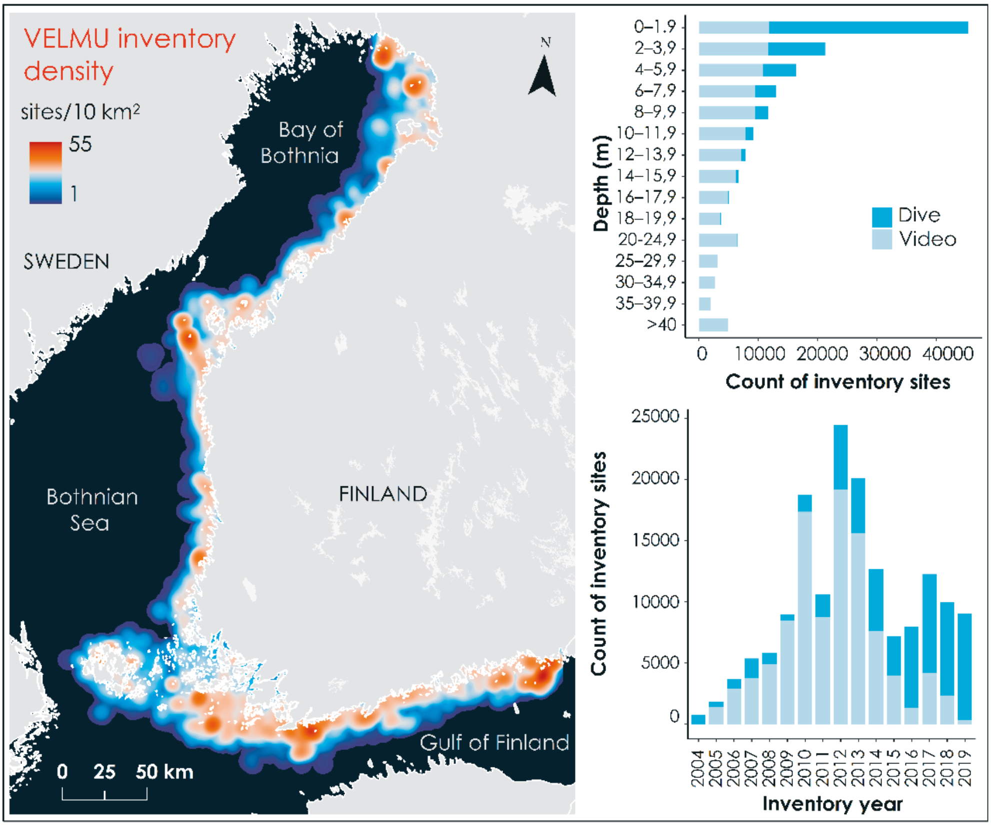

Figure 2. The map on the left shows where VELMU inventories have taken place between 2004 and 2019, represented as density of underwater inventory sites per 10 km^2. The upper right panel shows the count of VELMU inventory sites collected from different depth zones, with the two main VELMU methods, scientific diving (Dive) and video observation methods (Video). "Dive" includes all the VELMU inventory methods where species identification is possible to the species level. The lower right panel represent VELMU inventory years 2004–2019 and the count of data collected based on the dive and video inventory methods.

or vertical 1 m, from inspection squares of 1, 2, or 4 m^2. Drop-videos record approximately 20 m^2 of seabed, and coverages of species and seabed substrates are analyzed later from the videos. Overall, this extensive data offers an exceptional base for exploring questions regarding spatial ecology, conservation science, ecosystem-based management and changing environment.

In this thesis, VELMU data was used in case studies I, IV (species data), and III (ferromanganese concretions). Existing data on fish reproduction areas (perch, smelt, zander), based on VELMU fish larvae samplings, was also used in study **I** (Kallasvuo et al. 2016). In addition, eight Habitats Directive marine habitats associated with "marine environments" were used in study **I**: Baltic esker islands (1610), boreal Baltic islets (1620), boreal Baltic narrow inlets (1650), coastal lagoons (1150), estuaries (1130), large shallow inlets and bays (1160), sand banks (1110), and reefs (1170). Habitats were based on existing models and expert delineations reported for the EU in 2013 (EEA 2013, Rinne et al. 2014, Kaskela and Rinne 2018).

2.2.2 Predictor variables

In the modelling, to draw any conclusions about habitat preferences of species, or the conditions where concretions form, information about the marine environment is required. Information available included, for instance, bathymetry, nutrient concentration, wave forcing, temperature, salinity, euphotic depth, oxygen variability and seabed substrates (studies **I**, **III** and **IV**).

In study **II**, measures describing seafloor ruggedness and complexity were derived from bathymetry, such as: bathymetric position indices (BPI) with varying search radii, depth-attenuated wave exposure (SWM(d)), topographic shelter index (TSI), arc-chord rugosity (ACR) and vector ruggedness measure (VRM). BPIs measures the bathymetric surface ratio higher/lower in relation to surrounding environments, SWM(d) estimates wave force, TSI differentiates wave directions and sheltering effects of islands, and ACR and VRM describe seascape rugosities.

For the scenario modelling study **IV**, euphotic depth (Z_{eu}) – the depth where radiation has dropped to 1% of the surface radiation levels – was derived from Envisat-MERIS (Medium Resolution Imaging Spectrometer) satellite images for the summer periods (May–September) 2003–2011. The calculation of Z_{eu} layer was based on optical models with concentrations of total suspended matter, chlorophyll-*a*, humic substances as well as sun altitude angle and specific inherent absorption and scattering coefficients. All predictors utilized in studies **I**–**IV** are summarized in Table 1.

2.2.3 Anthropogenic stressors

SDMs describe the ecological niche of a species, which is related to environmental tolerances and habitat preferences (section 1.5). A major challenge is to determine how anthropogenic activities (such as coastal construction) change the inhabiting environment of species, as monitoring data before and after the activity is seldom available. Moreover, how intensities of resulting impacts are defined, causing either destruction, degradation or impairment, depends both on species and the habitat in question. Therefore estimates of cumulative impacts on marine biodiversity are usually based on expert knowledge (HELCOM 2018b). Because of difficulties in quantifying subtle or indirect effects of human activities on the marine environment, only activities leading to severe seabed modification, i.e. habitat loss and habitat degradation, were considered in the spatial prioritization of study **I** (section 2.4). Activities categorized as such were capital and maintenance dredging, proximity of harbours, and areas reserved for resource extraction and deposition of dredged materials. Data was collated from national databases and transformed into pressure layers following Sundblad and Bergström (2014) with minor modifications.

Table 1. Predictor variables developed for modelling species and concretion distributions, and hypoxia probabilities.

Predictor	**Unit**	**Explanation**	**Study**
Bathymetry	m	Depth information	I, II, III, IV
Bathymetric Position Index (BPI) with varying search radii	Index	An estimate of a higher topographic features than the surrounding environment, search radius 0.1, 0.2, 0.4, 0.8, 2, 4, 10, 20 km	I, II, III
Bottom temperature	˚C	Temperature (average, min, max) near the seabed (1 m) and temperature difference during the growing season	I
Bottom and surface salinity	PSU	Salinity near the seabed (1 m) and in the surface (1 m), corrected with the effects of rivers	I, III, IV
Chlorophyll *a*	$\mu g\ l^{-1}$	Mean chlorophyll *a* concentration in surface waters (0–5 m) during the growing season	III
Colored Dissolved Organic Matter (CDOM)	m^{-1}	Yellow substance; optically measurable component of the dissolved organic matter in the water	I, IV
Depth Attenuated Wave Exposure (SWM(d))	Index	Fetch + average wind speed + depth	I, II, III, IV
Distance to sandy shores	m	Closest distance to sandy shore	I
Euphotic depth	m	Euphotic depth and ± 50 % deviations from the present with 10 % intervals	IV
Geographical area	Index value	Geographical location of study area as an integer value	II
Iron content	$\mu g\ l^{-1}$	Cumulative and average concentration of soluble iron in the water column during 2004–2015	III
Oxygen variability, frequent and occasional hypoxia	$mg\ l^{-1}$ %	Continuous oxygen (average, min) content, probability of frequent and occasional hypoxia with O_2 thresholds 2 and 4.6 $mg\ l^{-1}$	I, III
Rocky, rock, sandy and soft substrates	%	The proportion of rocky (boulders and stones, 0.1–3 m), rock, sandy and soft (gravel, sand, silt, mud, clay; <60 mm) substrates	I, III, IV
Seascape rugosity: arc-chord rugosity (ACR) and vector ruggedness measure (VRM)	Index	Both measures evaluate surface ruggedness, ACR using a ratio of surface area, and VRM ratioa of cell center, local slope and aspect	II, III
Secchi depth	m	Secchi depth	I
Share of sea proportional to land area	%	Proxy for the complexity of archipelago; search radius 1, 5, and 10 km	I, III
Slope	◦	Slope of the seabed	I, III
Topographical shelter (TSI)	Index	Sheltering effect of topography	I, II, III
Total nitrogen and phosphorous content	$mg\ l^{-1}$	Total nitrogen and phosphorous content in the water column	I, III
Turbidity	FNU	Turbidity due to suspended material	I

2.3 Data pre-processing and modelling

To generalize the relationship between species, hypoxia, and concretions with their surrounding environments, the modelling method Gradient Boosting Machine and extended functions from Boosted Regression Trees (BRT) were utilized (Friedman et al. 2000, Breiman 2017) (for clarity, denoted only as BRT from hereon).

In study **I,** modelling relied mainly on dive data, and video sites were used only for clearly identifiable species. Additional national data repository, Hertta, was used for modelling invertebrate distributions, and for modelling macrophyte absences from deep seafloors. Most of the VELMU dive and video data are limited to rather shallow depths (typically 0 to 30 m). Thus, enough samples do not exist from deep areas (below 50 m). In order to avoid artefacts, a randomized absence dataset of benthic invertebrate samples (Ekman, Ponar, Van Veen and other grab samples for soft sediment sampling) for areas deeper than 50 m was utilized during the modelling process. These sites were used only as absences in macrophytes models, as habitat constraints and lack of light limit the distribution of macrophytes at such depths.

Randomized subsets of data (50–80%) were used to train the marine SDMs and tuning of model parameters in general was dependent on sample size and the prevalence of species, affecting the choice of learning rate. Higher tree complexities required slower learning rates and vice versa (common vs. rare species). Performances of SDMs were estimated with deviance explained, and the cross validated Area Under the Receiver Operating Characteristic curve (AUC), a measure of detection accuracy of true and false positives and negatives (Jiménez-Valverde and Lobo 2007). AUC values above 0.9 indicate excellent, of 0.7–0.9 indicate good and below 0.7 indicate poor predictions.

In study **II**, oxygen profile data was harvested from national, environmental data portals of Hertta (Finland) and SHARK (Sweden). Only August and September 2000–2016 were considered, as seasonal hypoxia occurs usually in late summer when water temperatures are higher (Conley et al. 2011). Ecologically meaningful limits to hypoxia were defined to be $O_2 <$ $2\ mg\ L^{-1}$ and $<4.6\ mg\ L^{-1}$. The former is a threshold where coastal organisms start to show severe symptoms of oxygen deficiency (Diaz and Rosenberg 1995, Diaz and Rosenberg 2008, Vaquer-Sunyer and Duarte 2008), and the latter has been estimated to be a minimum safe limit for species survival and functioning in benthic communities (Norkko et al. 2015).

As there exists no reference values for severity of hypoxia based on the frequency of hypoxic events, a site was categorized as “occasionally hypoxic”, if it experienced hypoxia at least once during the study period. If hypoxia was recorded in ≥ 20% of the visits, it was categorized as “frequently hypoxic”. This was considered ecologically relevant, as species can develop symptoms already from short exposure to oxygen deficiency (Villnäs et al. 2012, Norkko et al. 2015). The actual oxygen concentrations in the sediment, where benthic species live, are anyway probably lower than concentrations 1 m above the seafloor where the “bottom” water samples were taken. Four hypoxia models were trained based on the ecologically meaningful thresholds, and estimation of model predictive performances relied on the ability to discriminate a hypoxic site from an oxic one and simply with the percent correctly classified (Freeman and Moisen 2008).

In study **III**, ferromanganese concretion data from VELMU inventories were used to build models describing concretion distributions and abundances. For the abundance models, all coverages (0–100 %) were used in the analyses, whereas in the distribution models, four coverage thresholds were developed, as the detection accuracy may vary depending on the observation method in question. Four thresholds were: >0.1% (all presence observations), >10% (abundant concretions), >50% (substantial cover) and >70% (major concretion fields). Estimation of concretion models relied on AUC and true skill statistics (TSS) scores (Allouche et al. 2006). For the concretion abundance models (percent coverages 0.1–100 %) the coefficient of determination (R^2) and mean absolute error were calculated.

In study **IV**, data pre-processing followed similar patterns as in studies **I-III**. *Fucus* spp. (*F. vesiculosus* and *F. radicans*) are clearly identifiable species from both dives and videos, thus no selection between the two methods were made. However, only a randomly chosen 25% of the targeted video inventories was used in the modelling. As in study **I**, to correct the inventory bias from shallow areas, benthic invertebrate samples from depths 17–286 m were added to the fitting dataset as known *Fucus* spp. absences.

Scenario modelling may face a problem of "environmental novelty", meaning that model extrapolation does not work well if expected future environmental conditions do not exist in the training data. Thus, predictions outside the range where observations have been collected (be it either presence or absence), may be over- or underestimations (Elith et al. 2010). This was corrected in study **IV** with information about historical conditions, or "retrospective environment". Depth-penetration of *Fucus* spp. was remarkably deeper 100 years ago (Torn et al. 2006). To inform models in the model building with the past conditions, i.e. the historical depth-penetration of *Fucus* spp., a subset of presence observations was duplicated and used as pseudo-presences. Z_{eu} was multiplied by 1.25 and 1.5 to represent same sites as already observed in the inventories, but with an increased water transparency based on historical data.

In studies **I–IV** models were extrapolated to the full seascape at a resolution of 20 m and in studies **II** and **III** spatial predictions were repeated 10 times with randomly shuffled training datasets. In studies **II**, **III** and **IV**, probability predictions were dichotomized into binary presence/absence classes. Although this flattens the information content, it also facilitates the interpretation of results and is needed for management purposes. Dichotomization cut-offs are based on the confusion matrix, i.e., how well the model captures true/false presences or true/false absences. Usually the threshold is defined to maximize the agreement between observed and predicted distributions. Widely used thresholds, such as 0.5, can be arbitrary unless the threshold equals prevalence of presences in the data, i.e., the frequency of occurrences (how many presences of the total dataset) (Liu et al. 2005). In study **II** and **III**, the cut-off was based on an agreement between predicted and observed prevalence and thus represents a conservative estimate. In study **IV** the threshold was chosen to deliver equal sensitivity and specificity, meaning positive observations are just as likely to be wrong as negative ones (Freeman and Moisen 2008).

2.4 Spatial conservation prioritization

In study **I**, key areas for conservation were identified with the decision-support tool Zonation. Technically, Zonation operates on high-dimensional spatial data, concerning for instance biodiversity features (habitats, species, ecosystem services), costs, threats, or connectivity (Kareksela et al. 2013, Kukkala and Moilanen 2017, Verhagen et al. 2017, Virtanen et al. 2020). Zonation produces a balanced ranking across the landscape, by iteratively removing cells that can be lost with smallest aggregate loss for biodiversity. From a management perspective, areas receiving high rank values are key areas from conservation point of view - hosting various highly weighted and rare species, habitats and habitat types - and lowest degraded, pressurized areas, holding less ecological value, where management activities could be directed to, or where human activities could be allowed with minimized loss for biodiversity (Moilanen et al. 2005, Kareksela et al. 2013).

Zonation was used in identifying key areas for conservation and in evaluating the ecological coherence of current MPAs, and further suggesting expansion areas complementing the present MPA network. Marine SDMs (section 2.3), HD habitats, fish reproduction areas, and pressures (section 2.2) were used as inputs into the analyses.

An important first part of Zonation analyses is assigning weights for features going into spatial prioritization analysis. As a starting point, features can be equally weighted, although there are several reasons for elevating weights, such as species characterized as ecosystem engineers or species holding economic value (Lehtomäki and Moilanen 2013). In study **I**, a hierarchical way of assigning weights was adopted, in which relative aggregate weights 3:1:1 were assigned to species, HD habitats and habitat types based on 2018 threatened status assessment of IUCN Red List of Ecosystems, respectively. Weights were inclined towards species, as the number of species was higher than that of habitats in the analysis. Negative weights, for features thought to impact negatively on the ecological value of a site, were assigned to non-indigenous species (e.g. zebra mussel) and marine pressures, such as maintenance dredging and resource extraction.

Zonation requires information about how features are balanced during the analysis runs. Aggregation of biodiversity value was done with the additive benefit function, where feature performances are tracked along individual species-area curves, aiming to minimize aggregate expected extinction risk (Moilanen 2007). This is justified in situations where input data can be seen to act as surrogates for factors not directly represented by available data. As an output, Zonation produced a priority rank map, where cells were ordered with respect to each other. The ranking does not quantify solution quality in any absolute sense. Rather, directly associated performance curves summarize the conservation coverage that would be achieved in any top priority fraction selected from the priority rank maps. Key conservation value hotspots were identified by combining the priority rank outputs, describing the relative ranking balanced across features, and the weighted range-size rarity map, the weighted sum that emphasizes locations having many features in them. Integration of these two emphasizes species richness and ecosystem function compared to the priority rank map.

Connectivity is an integral part of spatial analyses, and an important component of spatial prioritization in marine environments, the relevance of it depending on however, species and the environment in question (Virtanen et al. 2020). Connectivity was induced into analyses using two basic options, matrix connectivity and edge removal, with the general objective of accomplishing aggregation that would facilitate the logistics of management decisions. Matrix connectivity identifies and enables connectivity of similar and adjacent habitats (Lehtomäki et al. 2009). A decay distance of 200 m was set for matrix connectivity between different Habitat Directive Annex I habitats, elevating priorities of for instance reefs and underwater parts of islets. Edge removal promotes maintenance of structural continuity of prioritized areas, as cells are ranked and removed from the edges of remaining areas.

Post-processing options of Zonation were used to estimate the quality of Habitat Directive Annex I habitats and each existing MPAs (HELCOM MPAs, national parks, Nature 2000 sites, nature reserves, private MPAs, Ramsar sites). After prioritization runs, landscape mask analysis (LSM) enables the evaluation of pre-specified areas (groups of grid cell) or area networks, to the level of individual features (Moilanen and Kujala 2014). LSM was used to identify good-quality habitat patches outside the existing MPA network and evaluate the quality of already established MPAs. Each individual habitat and MPA was evaluated based on the mean rank – the average of pixel-specific rank values from the priority rank map, and feature density of area i (FD_i) – the feature distribution sum of the area divided by the distribution sum expected if all features were evenly distributed across the seascape:

$$FD_i = \frac{DS_i * C}{A_i * TDS}, \text{ where}$$

DS_i = distribution sum of focal area i, C = number of effective cells in the whole seascape, A_i = number of cells in the focal area, and TDS = total distribution sum of all features across the entire study area.

Finally, illustrative, potential candidates were identified to complement the existing MPA network, based on a hierarchic prioritization that specifically accounts for the present MPA network. For illustration, potential MPA expansion candidates were identified taking the highest ranked 3 % of areas outside the present MPA network, then filtering out areas less than 1 km^2 in size to emphasize large expansion areas, leading to a proposal for an 1 % net expansion of Finnish marine protected sea network.

3 Results and discussion

3.1 Key areas for conservation

Case study **I** identified key areas for conservation, evaluated the ecological coherence of the Finnish MPA network, and suggested potential expansion candidates to fix its gaps in protection. For this, SDMs were built for alga, bryophytes, vascular plants and invertebrates, and together these SDMs represent over 200 species and ~100 taxa: (*i*) most common and widespread species (e.g., clasping-leaf pond-weed *Potamogeton perfoliatus*), (*ii*) key and habitat-forming species (e.g., bladder-wrack *Fucus* spp.), (*iii*) threatened species (e.g., Baltic water-plantain *Alisma wahlenbergii*), (*iv*) rare or sparsely occurring species (e.g., eelgrass *Zostera marina*), (*vi*) non-indigenous species (e.g., zebra mussel *Dreissena polymorpha*) and (*vii*) threatened habitat types based on 2018 threatened status assessment based on IUCN Red List of Ecosystems (e.g., dominating benthic habitats characterized by red algae) (Kontula and Raunio 2019).

The SDMs performed generally well, with median deviance explained 71–87 % on withheld data and AUC values above 0.7 for all models. Models were based on best underwater data available and on modelling methods prominent in broad SDM literature (e.g. Elith et al. 2010, Robinson et al. 2011, Guisan et al. 2013, Breiner et al. 2015, Morán-Ordóñez et al. 2017, Norberg et al. 2019).

The SDMs developed, as well as spatial layers for HD habitats, fish reproduction areas and anthropogenic stressors (section 2.2), were used as input data for identifying key areas for conservation. The unconstrained spatial prioritization run, "clean slate solution", shows where the highest concentrations of marine biodiversity features are. High priorities correspond to ecologically highly relevant areas, and host comparatively many rare and threatened species, functionally important (highly weighted) species and habitats, well-connected habitat complexes, and species-rich environments.

High priority areas found by this analysis can be characterized as shallow, diverse environments, with a favourable amount of light and limited anthropogenic disturbance. Areas worth mentioning include shallow bays and river estuaries in the northern Bothnian Bay, pristine reef environments in the northeastern parts of Åland main island, sandbanks in the Archipelago Sea, diverse islet and reef environments west from the Hanko Peninsula and species-rich shallow bays in the Gulf of Finland. Establishing a *de novo* MPA network from this "clean slate solution", would lead to high conservation gains, as 80 % of the distributions of marine biodiversity features would become covered.

However, as MPAs have already been established in the Finnish sea areas, a more realistic approach would be the further development of the existing MPA network with highest-quality expansion sites, efficiently filling ecological and geographical gaps in protection. As it turns out, the present MPA network misses out on key species and habitats, as on average only 27 % of the distributions of the marine biodiversity features are located inside the current MPA network (Fig. 5b in study **I**).

This is not surprising, as at the time of MPA establishments there was limited knowledge of underwater species and habitats.

An expansion of the MPA network by only one percentage point in area (815 km^2) would double the mean marine biodiversity feature coverage (Figure 6B and Supplementary Figure S1 in study **I**). This suggests that well-informed MPA expansion has the potential to considerably improve the ecological performance of the existing MPA network. An illustrative set of MPA expansion candidates were identified, complementing the current MPA network: adjacent areas close to current MPAs as well as independent new MPAs (Figure 3).

In general, new areas were suggested further away from areas pressurized by various human activities, such as cities and harbors. Geographically, a large part of the individual MPA expansion candidates were identified around the Åland main island, in areas relatively less impacted by eutrophication and anthropogenic activities. These areas were also identified as ecologically relevant in a recent national survey (Rinne et al. 2019), and sustain, for instance, high occurrence rates of *Fucus* spp. (Rinne and Salovius-Laurén 2019). Concentration of new MPA expansion candidates around the Åland main island is further supported by a recent biophysical

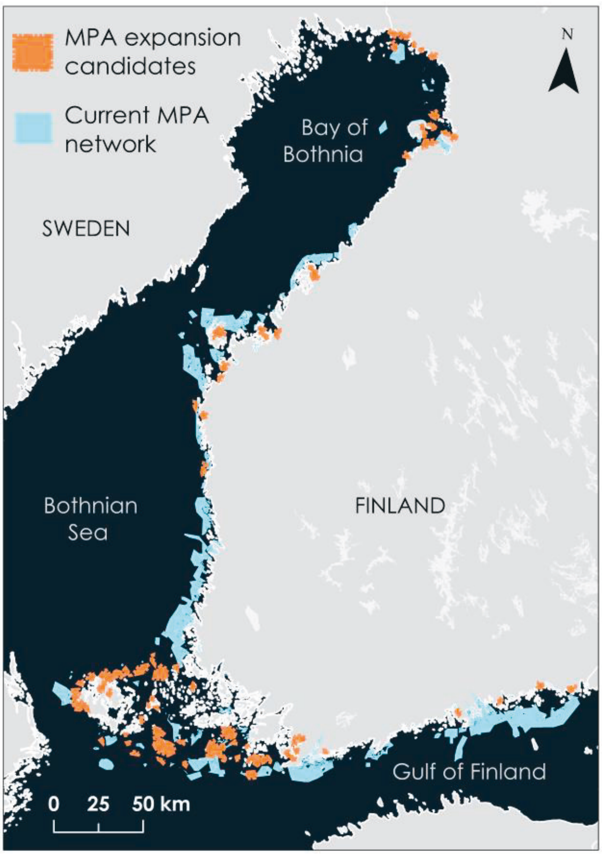

Figure 3 The current Marine Protected Areas (MPAs) and suggested MPA expansion candidates. Figure redrawn from study **I**.

modelling study, aiming to maximize connectivity between HELCOM MPAs, by Jonsson et al. (2020), where MPA expansion candidates mostly coincide with the results of this study. Although studies were based on different methods and data, this compatibility most likely results from the fact that high connectivity correlates with biodiversity, as high quality habitats tend to both export and receive dispersing propagules (Jonsson et al. 2020, Virtanen et al. 2020).

A peculiarity for Finland is private water ownership. A large part of coastal waters is owned by private land owners, as well as municipalities, cities and in some cases private enterprises. As much as 71 % of the MPA expansion candidates are located on private waters. With a limited amount of state-owned area available for MPA expansion, private marine protection as well as “other effective area-based conservation measures” (OECMs) should be promoted, to reach the goals of CBD’s post-2020 strategy (EEA 2020). Private marine conservation may increase the total area under protection, increase environmental awareness, and enhance the dialogue, and co-operation, between the private sector, key stakeholders and conservation management. However, designation and implementation of private MPAs depends on the capacity and willingness to protect and manage MPAs, and on the resources of conservation institutions to monitor the effectiveness of private conservation actions (Bottema and Bush 2012, Farmer et al. 2017, Drescher and Brenner 2018).

Relying on the extensive VELMU data, study **I** is the first comprehensive assessment of the ecological effectiveness of MPAs within the Baltic Sea area. Surprisingly, only a few prior attempts exist. For instance, Sundblad et al. (2011) evaluated the ecological coherence of MPAs based on recruitment habitats of common fish species, and Jonsson et al. (2020) estimate the connectivity of HELCOM MPAs based on biophysical modelling. This scarcity of MPA research is most likely linked to the lack of detailed data on species and habitats, and suitable analysis paths for comprehensive evaluation of MPAs, as also suggested by the HELCOM ecological coherence assessment of the Baltic Sea MPAs (HELCOM 2016).

Based on the findings of study **I** the majority of ecologically most important areas is located outside the current MPA network. Consequently, the role of MSP in safeguarding marine biodiversity becomes elevated, as decisions on the use of marine space need to consider important areas outside legal protection, including many privately-owned areas.

3.2 Indicating areas for effective nutrient abatement

As biogeochemical modelling of hypoxia is challenging in coastal environments, study **II** tested if proxies describing seafloor complexity could explain the small-scale variation of coastal hypoxia and identify locations naturally prone to hypoxia development. The importance of the physical morphology of the seabed in hypoxia formation is intuitively obvious and has been suggested by several authors (Diaz and Rosenberg 1995, Virtasalo et al. 2005, Rabalais et al. 2010, Conley et al. 2011), but has nevertheless not been tested with actual data.

Recognizing that the enclosed nature of seafloors facilitates hypoxia formation, simple topographic parameters were developed for hypoxia models in the complex archipelagos of Finland and Sweden. A surprisingly large fraction (~ 80 %) of hypoxia occurrences could be explained by topographical parameters alone. Areas identified as prone to hypoxia were characterized by low exposure to wave forcing, high topographic shelter from surrounding land areas and isolation from the open sea, all probably contributing to longer water residence times in seabed depressions. Deviations from this pattern are most likely to be caused by directional, strong currents or by high nutrient loading and elevated primary production, either improving or worsening the oxygen status, respectively. Major nutrient sources, such as rivers, cities or intensive agricultural areas, potentially also induce hypoxia formation. However, in extremely complex archipelago areas, such as the ones in Finland and Sweden, physical factors limiting lateral and vertical movement of water probably facilitate, and in some areas even dictate, the development of hypoxia.

The most influential predictors, averaged across models, were depth-attenuated exposure (SWM(d)), followed by depth, and BPIs identifying wider sinks (Fig. 4, study **II**). This indicates that severe oxygen deficiency is more likely to develop in sheltered areas, where water movement is limited. Such areas are also usually afflicted by internal loading of phosphorus from sediments (Puttonen et al. 2014, Puttonen et al. 2016), although phosphorus can also be released from oxic sediments when organic matter decomposition is high (Walve et al. 2018). It is notable that coastal hypoxia was not directly dependent on depth. Hypoxia was common in shallow and moderate depths of 10–45 m, and, for instance in the Archipelago Sea, deep (60–100 m) "channels" are normoxic, as strong currents keep them oxygenated throughout the year (Virtasalo et al. 2005). Instead steep, isolated, and sheltered depressions become more easily hypoxic. The relatively high contribution of topographic shelter also indicates that height of islands creates shelters for wind-induced mixing of water, contributing to hypoxia formation. This was the case for example in the archipelago areas of western Gulf of Finland, where high islands surround the enclosed water bodies (Fig. 4, study **II**).

Areas topographically prone to hypoxia represent less than 25 % of the studied seascapes, and were concentrated on the western Gulf of Finland, the Finnish Archipelago Sea, the Stockholm archipelago and western Gulf of Finland. These areas are partly isolated from the deep areas of the central Baltic Sea and are characterized by complex topography. In contrast, around 10 % of areas in the eastern Gulf of Finland were vulnerable to occasional, moderate hypoxia ($O_2 < 4.6$ mg L^{-1}) but less to severe hypoxia ($O_2 < 2$ mg L^{-1}). This may be at least partly caused by the intermittent transport of anoxic waters from the central Baltic Sea, along the Gulf of Finland, into the shallow archipelago areas of the south-eastern Finland (Alenius et al. 2016).

Although hypoxic areas represent rather small geographical entities, even small-sized hypoxic depressions, especially if forming a 'hypoxic network', releasing nutrients into the water, may degrade the ecological status of a whole coastal area.

Ecological repercussions of even short-termed hypoxia may be profound to ecosystem functioning (Villnäs et al. 2013). Currently, ecologically most important areas are located in rather shallow environments (study **I**). These shallow areas are vulnerable to projected negative effects resulting from climate change, as water temperatures are on the rise, thus accelerating deoxygenation (Meier et al. 2011a, Breitburg et al. 2018). Oxygen deficiency has also been projected to develop faster in shallow, coastal systems than in the open sea (Gilbert et al. 2010, Altieri and Gedan 2015). Seasonal hypoxia may thus become an even more recurrent phenomenon in shallow areas above the thermocline in late summer.

Results of study **II** are generally in line with prior research, confirming that coastal hypoxia is a common phenomenon in the Baltic Sea (Conley et al. 2011), but ecologically relevant hypoxia may be more common than previously anticipated. Although extensive biogeochemical models have been developed for the main basins of the Baltic Sea (Meier et al., 2011b, 2012a, 2014), previous estimates of coastal hypoxia have relied on point observations (Conley et al. 2009, Conley et al. 2011), as biogeochemical modelling of hypoxia has its limitations in complex coastal areas. This study proposes a new approach for modelling coastal hypoxia, without data on currents, stratification, or biological variables, and without convoluted biogeochemical models, requiring intensive computational power, especially when run even on moderate resolution 3D grids. The approach developed here would be useful for targeting local nutrient abatement measures and is applicable in other low-energy and nontidal systems, such as large shallow bays and semienclosed sea areas elsewhere in the world.

3.3 Identifying locations for resource extraction

Study **III** explored the distribution of ferromanaganese concretions, which are at the moment a "data deficient" habitat type in the assessment of threatened habitat types based on the IUCN Red List of Ecosystems (Kontula and Raunio 2019). Moreover, the ecological role of concretions as a potential biogenic habitat remains undecided. Concretions are known to be widespread in the coastal waters, but more research efforts have been invested in deep-sea concretions (Gazis et al. 2018, Peukert et al. 2018). Concretions are of interest to the seabed mining industry, as they contain economically valuable and commercially exploitable metals (Hannington et al. 2017).

In study **III**, concretions were found adundantly from almost all sea basins, forming distinct belts extending from the Bothnian Bay to the Gulf of Finland. In the Kvarken and the Gulf of Finland, concretions form extensive fields. According to the results, at least 11 % of the Finnish seafloors host suitable environments for concretions to form. These findings show a much larger extent of concretions than previously reported (Glasby et al. 1997, Yli-Hemminki et al. 2016). To put this into geographical context, the projected distribution of concretion fields is larger than the total coverage of all marine Habitat Directive Annex I Habitats, which jointly cover only 6 % of the Finnish sea area (**I**).

Concretions were recorded in depths of

0–75 m together with various seafloor types, ranging from mud to rock. Denser concretion fields were mostly related to mid depths (in the Baltic Sea context) close to the slopes of the deeper basins. This could be caused by a specific chemical environment prevailing in these areas, such as hypoxic water originating from the deep basins occasionally flushing the slopes. Concretions are also more easily observed in areas, where sediment accumulation rates are low, and impacts from wave exposure high (Glasby et al. 1997, Zhamoida et al. 2007). As this study was based on visual observations only, concretions most probably were not detected in areas where waters are turbid or in environments where sedimentation rates leave concretions buried. This has one important implication: if a large part of concretions is buried under sediment, concretions may be even more common and widespread than reported in this study.

Frequently hypoxic areas seemed to be devoid of concretions, whereas the opposite was observed for areas suffering from occasional, moderate hypoxia (hypoxia models developed in study **II**). This can be explained by the fact that in anoxic and severely hypoxic conditions, concretions dissolve (Zhamoida et al. 2007, Yli-Hemminki et al. 2016). In contrast, the proximity of areas with oscillating hypoxia facilitates concretion growth by the transport of dissolved nutrients (Glasby et al. 1997). This explains why concretions tend to form on slopes and edges of larger depressions bordering anoxic areas, in close proximity to large hypoxic areas with potentially high phosphorus releases.

Concretions also deposit high concentrations of phosphorus (Baturin 2009), and it has been suggested that concretions in the Gulf of Finland contain 10 times more phosphorus than anoxic areas (Savchuk 2000, Lehtoranta and Pitkänen 2003). Climate change is projected to worsen the oxygen status of the Baltic Sea (Meier et al. 2011a), which may have an effect on the rate how fast concretions dissolve, and consequently to the rate of phosphorus release from concretions.

Concretions are reported here to occur extensively in the Finnish sea areas. Scattered observations have also been reported on the fringes of deeper basins in Sweden, Estonia and Russia, spanning areas hundreds of kilometers long within the Bothnian Sea and the Gulf of Finland (EMODnet 2019). While the results of study **III** can not be used to evaluate the vertical thickness of concretion fields, the sheer distribution range of concretions may make them rather tempting for economic purposes. Shallow-water concretions are not yet industrially exploited, but experimental extraction has already taken place in the eastern Gulf of Finland (Zhamoida et al. 2017). This raises questions about environmental effects of extensive exploitation of concretion fields, and other types of seabed mining, in particularly sensitive sea areas such as the Baltic Sea in general.

In order to examine the economic resource potential of ferromanganese concretions, the biogeochemical and ecological risks and potential impacts of large-scale extraction activities must be assessed (Kaikkonen et al. 2018). Ferromanganese concretions may serve as biogenic habitats for epibiotic species, but further research would be required. While there are no explicit studies of the relationship between concretions and individual species or biological diversity, it is obvious that they form three-dimensional, relatively stable structures, which might be populated by a variety of organisms that would not occur in areas mostly covered by soft sediments. Mining activities could be detrimental to the ecological status of such habitats.

3.4 Potential future changes in key communities

In study **IV**, potential changes in the distribution of habitat-forming *Fucus* spp. was modelled under different water clarity (Z_{eu}) scenarios, deviating from the present up to ± 50 % with 10 % intervals. Evaluated against validation data, the base model performance was good, with AUC 0.924 (SE ± 0.003) and TSS 0.69. Euphotic depth was the most influential predictor (28 %), followed by depth (27 %), surface salinity (18 %), unstable seabed substrates (17 %) and depth attenuated wave exposure (10 %).

In general, although *Fucus* spp. could penetrate deeper with increasing water clarity, the availability of suitable substrates limits vertical colonization. Consequently, proportional increases in the horizontal extent of *Fucus* spp. are larger in the outer than in the inner archipelago, due to the availability of suitable hard substrates. For instance, the southwestern parts of the Archipelago Sea and the outer archipelago of the Gulf of Finland had the greatest potential for gaining new *Fucus* spp. distribution areas with increasing water clarity, as suitable substrates prevailed deeper. Changes in the inner archipelago were less marked, as the proportional share of soft sediment types becomes higher (Figure 4). Decrease in water clarity would in turn lead to marked losses of *Fucus* spp. distribution. In the most extreme scenario, where water transparency decreases by 50 %, the distribution extent of *Fucus* spp. would narrow down by 59–100 % in the Kvarken, 55–70 % in the Gulf of Finland, 37–66 % in the Bothnian Sea, and 24–53 % in the southwestern parts of the Archipelago Sea (Figure 4). Moreover, steep profiles of shorelines and underwater parts of island prevail in some areas of the inner archipelago, such as in the western Gulf of Finland, which undermines the horizontal expansion of *Fucus* spp. with increasing light, compared to gently sloping, illuminated seafloors, which are typical for instance in parts of the outer archipelago of the Bothnian Sea and the Archipelago Sea.

Achieving GES of surface waters as defined by WFD would lead to positive change in the water clarity, consequently benefiting *Fucus* spp. and other macroalgae living on hard substrates. However, large variation exists in the eutrophication status between different WFD coastal types. National targets for GES have been set for each WFD coastal types (Aroviita et al. 2012). To achieve GES, Z_{eu} should increase by 7–59 %, depending on the coastal type (Table 2).

The largest improvement in water clarity is required in the Gulf of Finland (45–59 %) and in the Southwestern archipelago (33–50 %), whereas in the outer parts of the Bothnian Sea and Kvarken, the change needed to reach GES would be only 7–12 %. For instance, the Gulf of Finland and Archipelago Sea suffer from eutrophication and high water turbidity, and as a result, *Fucus* spp. and other macroalgal species are presently not able to utilize the

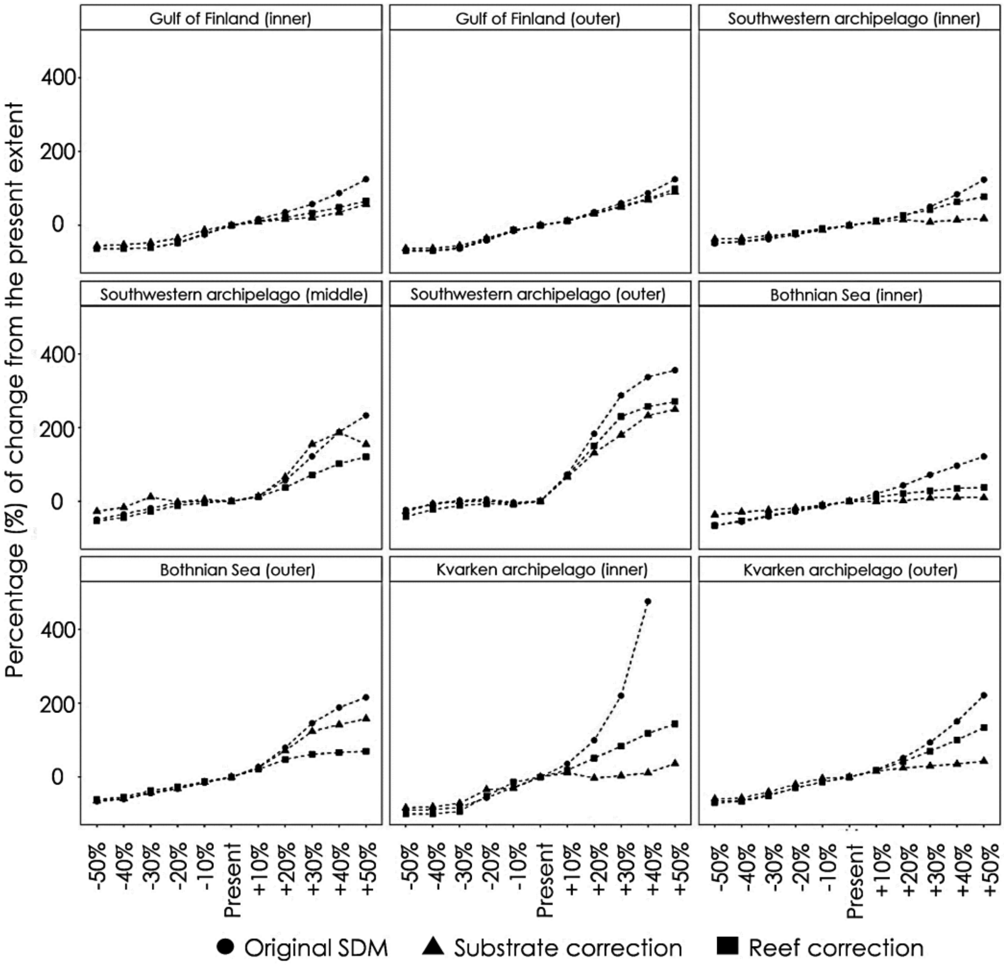

Figure 4. Relative potential distribution area of Fucus spp. compared to predicted present 2003–2011 distribution for the WFD coastal water types using three different methods: original area predicted by SDM, substrate correction method and reef layer method. Original SDM predicts area as is, substrate correction applies correction using substrate data from random videos and reef method extracts only *Fucus* spp. areas that are located on reefs. The scenarios on x-axis present the change of Z_{eu} from the present state in percentages. Figure redrawn from study IV.

full breadth of their potential occurrence area due to water turbidity (Rinne and Salovius-Laurén 2019).

Decreasing water turbidity has already limited the depth penetration of *Fucus* spp. in the western Gulf of Finland, as the lower limit of *Fucus* spp. distribution has shifted further towards shallow waters, as shown by monitoring studies (Ruuskanen 2016). Thus, such areas would benefit from targeted nutrient abatement measures, since habitat *gains* would be largest. This would not only benefit *Fucus* spp., but also the flora and fauna associated with *Fucus* spp. belts. At the other end of the spectrum is Kvarken and the Bothnian Sea, which are in comparatively good state and suffer less from eutrophication.

Table 2. Mean euphotic depth (Z_{eu}) in 2003–2011, required change needed to achieve good ecological status (GES) of Z_{eu} as defined by Water Framework Directive (WFD) and potential Fucus spp. distribution gains (%) if GES of Z_{eu} is achieved. Table modified from study **IV.**

WFD coastal types	Mean Z_{eu} (m) 2003 - 2011	GES of Z_{eu} (m) (and change needed to achieve it as %)	*Fucus* spp. distribution gain (+ %) if GES of Z_{eu} is achieved
Gulf of Finland (inner)	6.0	9.6 (+ 59 %)	> 57–125 %
Gulf of Finland (outer)	7.9	11.4 (+ 45 %)	80–106 %
Southwestern archipelago (inner)	6.6	9.8 (+ 50 %)	18–124 %
Southwestern archipelago (middle)	8.9	11.8 (+ 33 %)	80–164 %
Southwestern archipelago (outer)	10.6	14.0 (+ 33 %)	196–302 %
Bothnian Sea (inner)	7.1	9.2 (+ 29 %)	8–69 %
Bothnian Sea (outer)	9.9	10.8 (+ 9 %)	19–24 %
Kvarken (inner)	6.5	7.0 (+ 7 %)	9–25 %
Kvarken (outer)	9.0	10.0 (+ 12 %)	18–26 %

Consequently, greatest distribution *losses* due to worsening eutrophication could be seen exactly there, as *Fucus* spp. and other macroalgal species are currently able to utilize the full breadth of their potential distribution zone. This is also supported by the findings of a recent study by Rinne and Salovius-Laurén (2019), where *Fucus* spp. were found to be in relatively good status in the Bothnian Sea and northern parts of the Åland Sea, with higher occurrence rates and deeper depth-penetration.

It is also notable that *Fucus* spp. communities in the Kvarken and Bothnian Sea will probably be sensitive to projected oceanographic changes induced by climate change (Andersson et al. 2015, Vuorinen et al. 2015). For instance, Jonsson et al. (2018) demonstrated that *Fucus* spp. habitats are expected to shrink dramatically due to declining salinity levels and consequent habitat fragmentation, and Takolander et al. (2017b) showed that *Fucus* spp. may be vulnerable to low salinity, especially if subjected to high temperatures even for relatively short periods.

The necessity to preserve *Fucus* spp. in the Kvarken and Bothnian Sea is further emphasized by the recent declines of *Fucus* spp. in other sea areas, especially in the outer Archipelago Sea (Vahteri and Vuorinen 2016), where the potential for *Fucus* spp. growth may be hampered by the high exposure gradient, grazing pressure by *Idotea balthica*, and by competition with filamentous algae (or a combination of these) (Berger et al. 2003, Nilsson et al. 2004, Jonsson et al. 2006). Another plausible reason for the inability of *Fucus* spp. to recolonize its former distribution areas in the outer Archipelago Sea is limited connectivity. High habitat fragmentation and consequent habitat isolation in these areas may exceed the relatively short dispersal abilities of *Fucus* spp., which usually are less than 10 km (Jonsson et al. 2018).

Thus, considering these current and future progressions, the most viable habitat areas for *Fucus* spp. populations in the future may well be in the Kvarken and in the Bothnian Sea, if projected declines in salinity conditions will not be realized.

3.5 Uncertainties and methodological challenges

Modelling has always the problem of uncertainty around it, as no model can fully describe the complexity and dynamics of the natural world. Models are only as good as the data underlying them. Especially in marine environments, assembling a representative set of reliable species occurrence data can be challenging. In this thesis, an unusually large amount of spatial data was used for modelling the current and future distribution of species, occurrences of ferromanganese concretions and probabilities of hypoxia development. Models were based on information sampled using standardized methods from tens of thousands of sites visited, where species (or concretions) were either recorded present (with percent cover assessed) or absent. Thus, the breadth and amount of data was substantial for developing statistically sound models. Nonetheless, there remain various sources of errors inherent in the data, which should be acknowledged.

Uncertainties associated with the spatial data arise from interpretation errors (e.g. subjective sampling), locational uncertainty (e.g. inaccurate georeferencing), sampling biases (e.g. fewer samples in deeper, offshore areas), varying sampling intensities (e.g. gridded vs. random observations), missing environmental predictors (e.g. wintertime ice scouring leading to habitat destruction), and temporal uncertainty (e.g. outdated species inventories).

Subjective sampling may have caused taxonomic survey errors or biases in the reported percent cover of species (or concretions). This is an intrinsic problem of all underwater inventory programmes operating in aquatic environments, where water clarity challenges visual interpretation. However, in situations where species identification is not 100 % reliable, a diver takes a sample of the species in question and does the identification later. In the case of video data, this is of course not possible. Moreover, taxonomic identification to the level of species is not always possible from videos (except for macroscopic species) and reported percent coverages should be interpreted with some caution. Consequently, only a small part of video data was utilized in models developed in studies **I, III** and **IV**. In study **III**, subjective sampling uncertainties were addressed by varying percent thresholds of reported concretions, and by stacking predictions from replicate data sets used for model building (as also in study **II**).

Locational uncertainties may arise from errors in georeferencing, resulting from inaccurate precision of GPS positioning and boat movement. Positioning accuracy also decreases with depth. This is a problem if the maximum error in location where species is identified exceeds the resolution of environmental predictors. This was not the case with VELMU data, as the locational error does not exceed the predictor grain size of 20 m. Locational uncertainties only become an issue for fine-scale predictions (e.g. couple of meters), and in models built with smaller sample sizes (Mitchell et al. 2017).

Opportunistic sampling strategies may not represent the true species-environment relationship. VELMU inventories have mostly followed random stratified sampling strategies, except for targeted inventories, and have concentrated less on deep (>50m) areas. Sampling biases and varying sampling intensities were dealt with in the modelling by using random subsets of data (**I**–**IV**), creating pseudo-absences to less visited areas, such as deep (>50m) offshore areas (**I** and **IV**), by handling sampling differences between Sweden and Finland (and WFD areas), by treating study areas as separate area in the model building (**II**), and by addressing spatial autocorrelation by introducing a residual autocovariate term to final models (**III**) (Crase et al. 2012).

Temporal uncertainties may have compromised model validity in locations where the suitability of the environment for species occurrence has changed considerably after species was observed. Community compositions, species ranges, habitats and environments may also change over time, and thus models may not fully represent the changed conditions. To describe species-environment relationship correctly, synoptic high-resolution environmental (predictor) data, long-term biodiversity monitoring and physiological experiments, as well as accurate information about how threats (pressures, stressors) modify habitats, would be desirable, but is unfortunately rarely available.

Inadequate relevance of available predictor variables may pose challenges for fine-scale, spatially explicit models. The bathymetry and substrate information are often inaccurate, due to the lack of data and military restrictions. The predictors used here cover a wide breadth of environmental factors affecting species distribution and habitat preferences (Table 1). Model performances throughout this thesis were high, which also suggests that predictors work at the seascape scale.

The SDMs capture the species-environment relationship in the absence of disturbances. Coastal areas are mostly shaped by various human activities, and by pressures they are causing on organisms, which are not necessarily captured by the abiotic predictors derived from water quality monitoring studies. Moreover, species inventories are more inclined towards areas with less influence from human presence. Emphasis should be placed on collecting species data from both pristine and disturbed environments, and on the derivation of near real-time (e.g. satellite-based) environmental data.

In a few years´ time, remote sensing will probably revolutionize the field of marine ecological modelling in a similar manner as in the terrestrial realm, where remotely derived predictors have significantly improved understanding of species distributions (He et al. 2015). High-resolution earth observation missions, such as Sentinel-2 (10–60 m), already provide near-real time data on marine areas, and include variables such as water clarity, enabling the development of more refined marine species distribution models. High temporal and spatial resolution of remotely sensed products will probably also enable the before/after analyses of intensities and extents of destructive human activities, which will make visible the effects of anthropogenic activity on the ecological state of the marine environment.

4 Conclusions and future perspectives

Seascape conservation and ecosystem-based marine management require spatially explicit data of areas worth conserving to support decision-making. This thesis aimed to show how extensive data combined with suitable spatial analysis can support seascape conservation and marine management, and to reaffirm the applicability of spatial analytical methods developed in the terrestrial realm to marine environments. In terms of applications, this thesis aimed to identify key conservation areas, pinpoint locations for efficient nutrient abatement measures and reveal areas suitable for economic resource extraction.

4.1 Applicability of results

In study **I**, the ecological coherence of Finnish MPA network was evaluated with spatial prioritization. Current MPAs leave almost three-quarters of ecologically and functionally important species occurrence areas unprotected, as in the past MPAs have been designated without much knowledge of underwater marine life. This suggests that the Finnish MPA network would benefit from further development. Expansion of the MPA cover by just 1%, from 10 to 11% area coverage using ideal expansion candidate sites would lead to extremely high relative conservation gains, as the mean conservation coverage of marine biodiversity feature cover would be doubled (study **I**, Fig. 6A-B). As the most promising expansion candidates are located on private waters, the need for spatial measures beyond state governed MPA network expansion is apparent. Especially the role of spatial planning decisions guiding the allocation of sea area for human activities becomes elevated.

Study **I** serves as a basis for identifying priority areas for spatial management measures, including establishment of new MPAs, and demonstrates the contribution of spatial prioritization to MSP. The results of study **I** can be and have already been used in various ways to promote conservation and sustainable use of sea areas. For instance, the key areas for conservation were used in the Finnish version of CBD EBSA (Ecologically or Biologically Significant Areas) (Johnson et al. 2018), called EMMA (ecologically significant underwater marine areas) (Lappalainen et al. 2020), which was further used in the development of national marine spatial plans according to the EU Marine Spatial Planning Directive. The results of study **I** could also act as a stimulus for promoting private MPAs, encourage private owners to protect their waters, and facilitate the conceptualization of private marine conservation.

In study **II**, areas naturally prone to hypoxia were identified using spatial analyses, borrowing concepts from landscape ecology. Based on the results, seafloor complexity facilitates, and even dictates, hypoxia development in enclosed, sheltered areas, where lateral movement of water is limited. Deviations from this pattern are a result of either strong mixing due to directional currents or high external nutrient loading, which may improve or worsen the oxygen status, respectively. The hypoxia modelling approach gives a practical baseline for various hypoxia-related studies and can support biogeochemical hypoxia models. Developed hypoxia models can be used to target nutrient abatement measures to locations, where they are most likely to be efficient. The results of study **II** can also explain why some areas are immune to nutrient abatement actions already taken. For instance, in areas naturally prone to severe hypoxia, and strong internal loading, measures focusing on limiting external nutrient loads may prove futile. In contrast, nutrient abatement could be much more effective in areas burdened by external loading but topographically less prone to hypoxia. These findings emphasize the role of sea governance: how should nutrient abatement measures be targeted cost-efficiently, to maximize benefits for the marine environment? Decisions are especially needed to conserve the remaining pristine marine areas and to rehabilitate ecosystems already suffering from eutrophication.

Study **III** demonstrated that ferromanganese concretions are more widespread than previously anticipated, occurring in over 11 % of the Finnish marine areas. However, these modelling results are based on visual inventories, suggesting that concretions can plausibly occur even more widespread than reported here, as concretions can also be buried in sediments. Because concretions hold high concentrations of minerals targeted by the emerging seabed mining industry, there may be economic opportunities for such extraction activities to take place also in the Baltic Sea. Results of studies **I** and **III** could guide detrimental mining activities to areas holding less ecological value, and to areas where concretions are abundantly found. However, the ecological role of concretions needs thorough investigation, as concretions may serve as biogenic habitats for various species. Only by combining sufficient ecological, geological and technological knowledge can environmentally sustainable marine resource governance be achieved.

Study **IV** showed that some areas would benefit more from nutrient abatement measures than others. Although *Fucus* spp. could penetrate deeper with increasing water clarity, the availability of suitable substrates limits vertical colonization in some areas. Due to the current eutrophication status in the Archipelago Sea and Gulf of Finland, the most viable populations of *Fucus* spp. may well be in the future in the Bothnian Sea and in the Kvarken, if declines in salinity conditions are not realized. In these areas decreases in water clarity would lead to marked losses of *Fucus* spp. and ecological functionality of the associated communities. This implies that *Fucus* spp. communities of these northern areas are especially vulnerable to further eutrophication, caused by projected environmental change.

Together these studies demonstrate that cross-disciplinary spatial analyses can both support decisions regarding marine conservation and sustainable use of marine areas and can also complement the success of other modelling methodologies (e.g. biogeochemical modelling) in complex coastal areas. Further, efficient management of marine areas requires integration of local management actions to wide-ranging policy processes. Ecosystem-based marine management needs to adopt and implement place-based management decisions that act at various spatial scales, operating at global (international policies and conventions), regional (EU directives, HELCOM), national (laws, decrees) and local (land/sea use zoning) levels.

4.2 Spatial analyses in the marine realm

This thesis has provided verifiable support for the fact that SDMs can be highly operational also in the marine realm. However, the success of marine SDMs is dependent on the characteristics of species occurrence data available (e.g. density and design of survey data, detectability of species, rarity of species, sample breadth of the total species range) and on the relevance of environmental predictors. Relevant proximal and distal environmental factors which regulate the occurrence of species have a larger influence on the success of SDMs than the type of modelling method chosen, and success of SDMs varies more between different species than between different modelling methods.

Based on the results of this thesis, modelling species distributions is feasible in marine environments where distinctive ecological niches, i.e. environmental heterogeneity, confine species occurrences, following partly from strong horizontal (increasing/declining by latitude/longitude), vertical (increasing/declining by depth) and distance-based gradients (increasing/ declining by distance). Marine SDMs also benefit from predictors regulating species distributions at different spatial scales, varying from local (e.g. substrate type) and seascape scales (e.g. turbidity) to regional scales (e.g. salinity).

While various environmental predictors in the marine realm have terrestrial analogues (e.g. bathymetry model vs. elevation model), environmental predictors in the marine realm can be temporally more dynamic than in terrestrial environments. For instance, turbidity and salinity near river estuaries are highly fluctuating and depend on freshwater outflow. In such instances, the ecological tolerance of a species to the environmental predictor should be evaluated over a long period, e.g. from water quality monitoring surveys or from satellite-derived environmental products. Especially for perennial species, the environmental conditions also outside the main growing season should be considered in determining the niche of the species.

As a recommendation, time and effort should be reserved to the quest for relevant environmental predictors, as in the marine realm predictors usually rely on 3D hydrodynamic-biogeochemical models at a grain and extent size (few nautical miles, basin-scale) not necessarily useful for developing fine-scale SDMs. For instance, various 3D models leave out shallow areas due to the complexity of coastal and archipelago zones, although these are the areas where various marine organisms live (**I**, **IV**) in close interaction with anthropogenic influences.

SDMs are almost always a means to an end, not the goal itself, as SDMs are used for instance in conservation planning, risk assessments, and in understanding species invasions and range shifts (Glardon et al. 2008, Martínez et al. 2015, Giakoumi et al. 2016, Oh et al. 2017, Duarte et al. 2018). This thesis has also illustrated that marine SDMs are useful in conservation planning and in the evaluation of the ecological coherence of MPAs. Still, analyses could be further expanded by adding information on ecosystem services, economics and marine connectivity dependent on species traits (cf.

Jonsson et al. 2020).

Most importantly, adding accurate and timely information of the pressures and disturbances that marine species and habitats face, would improve the accuracy of the description of the state of the marine ecosystem. Currently, most threat layers that enter spatial prioritization are constructed based on expert opinion without support from empirical data, and the effects of pressures on species and habitats, such as intensity and longevity, remain unclear. Impacts of the pressures resulting from various human activities could be gathered from various sources, such as scientific reviews and meta-analyses, technical reports and environmental impact assessments. Each pressure and disturbance layer could be individually coupled to species and habitats (e.g., via SDMs), due to the differences in responses of species and habitat to various pressures. Together these improvements would lead to a much more realistic depiction of key conservation areas and would be of utility to decision making around spatial conservation and marine management.

4.3 Future perspectives

The Baltic Sea is changing rapidly, as heat waves, declining salinity levels, increasing hypoxia and eutrophication reshape marine ecosystems and habitable environments, as demonstrated by coupled oceanographic-hydrodynamic biogeochemical modelling (Belkin 2009, Meier et al. 2011a, Meier et al. 2012b, Andersson et al. 2015, BACC 2015, Humborg et al. 2019). Thus, modelling species ranges conditional on projected change should be a research priority. Nevertheless, there are scarce examples of such research, and presently available work has concentrated on modelling range shifts for a small number of species (Jonsson et al. 2018, Kotta et al. 2019). Modelling climate change impacts for a broad range of species could provide important insight into the sensitivity, resilience, and extinction risk of species in relation to projected changes, as well as to potential changes in the functionality of marine ecosystems.

While SDMs predict the occurrences of individual species, recent methodological advances have enabled the simultaneous modelling of joint responses of multiple species to the environment. One of these methods is hierarchical modelling of species communities, which integrates (partially correlated) community-level responses to the environment, information on species traits, biotic interactions and phylogenetic relationships across various spatio-environmental scales (Ovaskainen et al. 2017). Topical questions could include: how similarities between marine communities depend on environmental similarity and geographical distance, or how much variation in marine species communities is explained by species traits and biotic interactions across varying spatial scales.

Identification of potential new conservation areas and marine biodiversity prioritization are of use also in ecological impact avoidance, where ecologically harmful activities are avoided in high-priority areas and directed to areas of less ecological value. For instance, “inverse spatial conservation prioritization” can be used to identify potential areas for economic development, while at the same time limiting environmental effects of the development activity (Kareksela et al.

2013). One of the next continuations from here could be to optimize potential areas for offshore wind farms, by combining the existing underwater knowledge with the economic feasibility of offshore wind energy, together with the societal and ecological impacts of such infrastructure development.

Another broadly useful continuation of study **I** would be the inclusion of set of species- and habitat-specific impacts of pressure and disturbance layers resulting from various human activities (see previous section). Interest in the addition of marine ecosystem services into conservation planning analysis is also apparent. Currently the concepts of marine ecosystem services and marine ecosystem accounting are being developed, and certain habitat types and functions of species groups are being tied to specific ecosystem services, after which the economic value of the ecosystem service provision can be calculated. Inclusion of ecosystem services would advance spatial planning processes and promote sustainable marine management.

References

Agardy, T., di Sciara, G.N. and Christie, P. (2011) Mind the gap Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy 35(2), 226-232.

Airoldi, L., Balata, D. and Beck, M.W. (2008) The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. Journal of Experimental Marine Biology and Ecology 366(1-2), 8-15.

Alenius, P., Myrberg, K., Roiha, P., Lips, U., Tuomi, L., Pettersson, H. and Raateoja, M. (2016) Gulf of Finland Physics: The Gulf of Finland assessment. Raateoja, M. and Setälä, O. (eds), pp. 42-57.

Allouche, O., Tsoar, A. and Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43(6), 1223-1232.

Altieri, A.H. and Gedan, K.B. (2015) Climate change and dead zones. Global Change Biology 21(4), 1395-1406.

Andersen, J.H., Carstensen, J., Conley, D.J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B.G., Josefson, A.B., Norkko, A., Villnäs, A. and Murray, C. (2017) Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. Biological Reviews 92(1), 135-149.

Andersen, J.H., Halpern, B.S., Korpinen, S., Murray, C. and Reker, J. (2015) Baltic Sea biodiversity status vs. cumulative human pressures. Estuarine, Coastal and Shelf Science 161, 88-92.

Andersson, A., Meier, H.E.M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., Legrand, C., Figueroa, D., Paczkowska, J., Lindehoff, E., Tysklind, M. and Elmgren, R. (2015) Projected future climate change and Baltic Sea ecosystem management. Ambio 44 Suppl 3(Suppl 3), 345-356.

Araújo, M.B., Anderson, R.P., Márcia Barbosa, A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E. and Rahbek, C. (2019) Standards for distribution models in biodiversity assessments. Science Advances 5(1), eaat4858.

Aroviita, J., Hellsten, S., Jyväsjärvi, J., Järvenpää, L., Järvinen, M., Karjalainen, S.M., Kauppila, P., Keto, A., Kuoppala, M. and Manni, K. (2012) Ohje pintavesien ekologisen ja kemiallisen tilan luokitteluun vuosille 2012–2013− päivitetyt arviointiperusteet ja niiden soveltaminen.

Atkins, J.P., Burdon, D., Elliott, M. and Gregory, A.J. (2011) Management of the marine environment: Integrating ecosystem services and societal benefits with the DPSIR framework in a systems approach. Marine Pollution Bulletin 62(2), 215-226.

BACC (2015) Second assessment of climate change for the Baltic Sea basin, SpringerOpen.

Ball, I., Possingham, H. and Watts, M. (2009) Spatial conservation prioritisation:

Quantitative methods and computational tools. Moilanen, A., Wilson, K. and Possingham, H. (eds), pp. 185-195, Oxford University Press, Oxford, UK.
Baturin, G. (2009) Geochemistry of ferromanganese nodules in the Gulf of Finland, Baltic Sea. Lithology and Mineral Resources 44(5), 411-426.
Belkin, I.M. (2009) Rapid warming of large marine ecosystems. Progress in Oceanography 81(1-4), 207-213.
Berger, R., Henriksson, E., Kautsky, L. and Malm, T. (2003) Effects of filamentous algae and deposited matter on the survival of Fucus vesiculosus L. germlings in the Baltic Sea. Aquatic Ecology 37(1), 1-11.
Bigagli, E. (2015) The EU legal framework for the management of marine complex social–ecological systems. Marine Policy 54, 44-51.
Bolam, S., Rees, H., Somerfield, P., Smith, R., Clarke, K., Warwick, R., Atkins, M. and Garnacho, E. (2006) Ecological consequences of dredged material disposal in the marine environment: a holistic assessment of activities around the England and Wales coastline. Marine Pollution Bulletin 52(4), 415-426.
Bonsdorff, E. (2006) Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. Journal of Experimental Marine Biology and Ecology 330(1), 383-391.
Bonsdorff, E., Blomqvist, E.M., Mattila, J. and Norkko, A. (1997) Coastal eutrophication: Causes, consequences and perspectives in the Archipelago areas of the northern Baltic Sea. Estuarine, Coastal and Shelf Science 44, 63-72.
Bonsdorff, E. and Pearson, T.H. (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: A functional-group approach. Australian Journal of Ecology 24(4), 312-326.
Bottema, M.J.M. and Bush, S.R. (2012) The durability of private sector-led marine conservation: A case study of two entrepreneurial marine protected areas in Indonesia. Ocean & Coastal Management 61, 38-48.
Breiman, L. (2017) Classification and regression trees, Routledge.
Breiner, F.T., Guisan, A., Bergamini, A. and Nobis, M.P. (2015) Overcoming limitations of modelling rare species by using ensembles of small models. Methods in Ecology and Evolution 6(10), 1210-1218.
Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M. and Zhang, J. (2018) Declining oxygen in the global ocean and coastal waters. Science 359(6371).
Brown, C.J., Smith, S.J., Lawton, P. and Anderson, J.T. (2011) Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuarine Coastal and Shelf Science 92(3), 502-520.
Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C. and Kornilovs, G. (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B: Biological Sciences 275(1644), 1793-1801.
CBD (2010) Aichi Biodiversity Targets. Convention on Biological Diversity.
Conley, D.J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B.G., Hietanen, S., Kortekaas, M., Kuosa, H., Markus Meier, H.E., Müller-Karulis, B., Nordberg, K., Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N.N., Rosenberg, R., Savchuk, O.P., Slomp, C.P., Voss, M., Wulff, F. and Zillén, L. (2009) Hypoxia-Related Processes in the Baltic Sea. Environmental Science & Technology 43(10), 3412-3420.
Conley, D.J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Haahti, B.M., Humborg, C., Jonsson, P., Kotta, J., Lannegren, C., Larsson, U., Maximov, A., Medina, M.R., Lysiak-Pastuszak, E., Remeikaite-Nikiene, N., Walve, J., Wilhelms, S. and Zillen, L. (2011) Hypoxia Is Increasing in the Coastal Zone of the Baltic Sea. Environmental Science & Technology 45(16), 6777-6783.
Conley, D.J., Humborg, C., Rahm, L., Savchuk, O.P. and Wulff, F. (2002) Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. Environmental Science & Technology 36(24), 5315-5320.
Cornu, E.L., Kittinger, J.N., Koehn, J.Z., Finkbeiner, E.M. and Crowder, L.B. (2014) Current practice and future prospects for social data in coastal and ocean planning. Conservation Biology 28(4), 902-911.

Crain, C.M., Halpern, B.S., Beck, M.W. and Kappel, C.V. (2009) Understanding and managing human threats to the coastal marine environment. Annals of the New York Academy of Sciences 1162(1), 39-62.

Crase, B., Liedloff, A.C. and Wintle, B.A. (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. Ecography 35(10), 879-888.

de Grunt, L.S., Ng, K. and Calado, H. (2018) Towards sustainable implementation of maritime spatial planning in Europe: A peek into the potential of the Regional Sea Conventions playing a stronger role. Marine Policy 95, 102-110.

Diaz, R. and Rosenberg, R. (1995) Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic macrofauna. Oceanography and marine biology 33, 245-303.

Diaz, R.J. and Rosenberg, R. (2008) Spreading dead zones and consequences for marine ecosystems. Science 321(5891), 926-929.

do Amaral, K.B., Alvares, D.J., Heinzelmann, L., Borges-Martins, M., Siciliano, S. and Moreno, I.B. (2015) Ecological niche modeling of Stenella dolphins (Cetartiodactyla: Delphinidae) in the southwestern Atlantic Ocean. Journal of Experimental Marine Biology and Ecology 472, 166-179.

Douvere, F. (2008) The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32(5), 762-771.

Drescher, M. and Brenner, J.C. (2018) The practice and promise of private land conservation. Ecology and Society 23(2).

Duarte, B., Martins, I., Rosa, R., Matos, A.R., Roleda, M.Y., Reusch, T.B., Engelen, A.H., Serrão, E.A., Pearson, G.A. and Marques, J.C. (2018) Climate change impacts on seagrass meadows and macroalgal forests: an integrative perspective on acclimation and adaptation potential. Frontiers in Marine Science 5, 190.

Dunn, D.C., Van Dover, C.L., Etter, R.J., Smith, C.R., Levin, L.A., Morato, T., Colaço, A., Dale, A.C., Gebruk, A.V., Gjerde, K.M., Halpin, P.N., Howell, K.L., Johnson, D., Perez, J.A.A., Ribeiro, M.C., Stuckas, H. and Weaver, P. (2018) A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining. Science Advances 4(7), eaar4313.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Forsterra, G., Galvan, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A. and Thomson, R.J. (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506(7487), 216-+.

EEA (2013) Reporting under Article 17 of the Habitats Directive (period 2007-2012), EIONET. European Topic Centre on Biological Diversity.

EEA (2015) State of the environment Report 2015 European Environment Agency, Copenhagen.

EEA (2020) Europe´s state of the environment 2020: change of direction urgently needed to face climate change challenges, reverse degradation and ensure future prosperity.

Ehler, C.a.F.D. (2009) Marine Spatial Planning: a step-by-step approach toward ecosystem-based management. 53.

Eilola, K., Meier, H.E.M. and Almroth, E. (2009) On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. Journal of Marine Systems 75(1), 163-184.

Elith, J., Kearney, M. and Phillips, S. (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1(4), 330-342.

Elith, J. and Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics 40(1), 677-697.

Elliott, M. (2011) Marine science and management means tackling exogenic unmanaged pressures and endogenic managed pressures – A numbered guide. Marine Pollution Bulletin 62(4), 651-655.

Elmgren, R., Blenckner, T. and Andersson, A. (2015) Baltic Sea management: Successes and failures. Ambio 44(3), 335-344.

Embling, C.B., Gillibrand, P.A., Gordon, J., Shrimpton, J., Stevick, P.T. and Hammond, P.S. (2010) Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (Phocoena phocoena). Biological Conservation 143(2), 267-279.

EMODnet (2019) EMODnet Geology, 2019. Marine Minerals, © EMODnet Geology, European Commission.

Eriksson, B.K., Sieben, K., Eklöf, J., Ljunggren, L., Olsson, J., Casini, M. and Bergström, U.

(2011) Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management. Ambio 40(7), 786.

Evans, D. (2012) Building the European Union's Natura 2000 network. Nature Conservation 1, 11.

Fabry, V.J., Seibel, B.A., Feely, R.A. and Orr, J.C. (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science 65(3), 414-432.

Farmer, J.R., Ma, Z., Drescher, M., Knackmuhs, E.G. and Dickinson, S.L. (2017) Private landowners, voluntary conservation programs, and implementation of conservation friendly land management practices. Conservation Letters 10(1), 58-66.

Fennel, K. and Testa, J.M. (2019) Biogeochemical Controls on Coastal Hypoxia. Annual Review of Marine Science 11(1), 105-130.

Fettweis, M., Baeye, M., Francken, F., Lauwaert, B., Van den Eynde, D., Van Lancker, V., Martens, C. and Michielsen, T. (2011) Monitoring the effects of disposal of fine sediments from maintenance dredging on suspended particulate matter concentration in the Belgian nearshore area (southern North Sea). Marine Pollution Bulletin 62(2), 258-269.

Freeman, E.A. and Moisen, G. (2008) PresenceAbsence: An R Package for Presence-Absence Model Analysis. Journal of Statistical Software 23(11), 1-31.

Friedman, J., Hastie, T. and Tibshirani, R. (2000) Additive logistic regression: a statistical view of boosting (with discussion and a rejoinder by the authors). The annals of statistics 28(2), 337-407.

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J. and Smith, A.D. (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12(2), 171-188.

Gammal, J., Norkko, J., Pilditch, C.A. and Norkko, A. (2017) Coastal Hypoxia and the Importance of Benthic Macrofauna Communities for Ecosystem Functioning. Estuaries and Coasts 40(2), 457-468.

Gazis, I.Z., Schoening, T., Alevizos, E. and Greinert, J. (2018) Quantitative mapping and predictive modeling of Mn nodules' distribution from hydroacoustic and optical AUV data linked by random forests machine learning. Biogeosciences 15(23), 7347-7377.

Giakoumi, S., Guilhaumon, F., Kark, S., Terlizzi, A., Claudet, J., Felline, S., Cerrano, C., Coll, M., Danovaro, R. and Fraschetti, S. (2016) Space invaders; biological invasions in marine conservation planning. Diversity and Distributions 22(12), 1220-1231.

Gilbert, D., Rabalais, N.N., Díaz, R.J. and Zhang, J. (2010) Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. Biogeosciences 7(7), 2283-2296.

Glardon, C.G., Walters, L.J., Quintana-Ascencio, P.F., McCauley, L.A., Stam, W.T. and Olsen, J.L. (2008) Predicting risks of invasion of macroalgae in the genus Caulerpa in Florida. Biological Invasions 10(7), 1147-1157.

Glasby, G., Emelyanov, E., Zhamoida, V., Baturin, G., Leipe, T., Bahlo, R. and Bonacker, P. (1997) Environments of formation of ferromanganese concretions in the Baltic Sea: a critical review. Geological Society, London, Special Publications 119(1), 213-237.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. and Buckley, Y.M. (2013) Predicting species distributions for conservation decisions. Ecology Letters 16(12), 1424-1435.

Halpern, B.S. (2014) Conservation: Making marine protected areas work. Nature 506(7487), 167-168.

Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C. and Selkoe, K.A. (2019) Recent pace of change in human impact on the world's ocean. Scientific Reports 9(1), 11609.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. and Watson, R. (2008) A Global Map of Human Impact on Marine Ecosystems. Science 319(5865), 948.

Halpern, B.S. and Warner, R.R. (2002) Marine reserves have rapid and lasting effects. Ecology Letters 5(3), 361-366.

Hannington, M., Petersen, S. and Krätschell, A. (2017) Subsea mining moves closer to shore. Nature Geoscience 10(3), 158-159.

Harley, C.D., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S., Rodriguez, L.F., Tomanek, L. and Williams, S.L. (2006) The impacts of climate change in coastal marine systems. Ecology Letters 9(2), 228-241.

He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S., Turner, W., Wegmann, M. and Pettorelli, N. (2015) Will remote sensing shape the next generation of species distribution models? Remote Sensing in Ecology and Conservation 1(1), 4-18.

HELCOM (2007) Baltic Sea Action Plan. HELCOM (ed).

HELCOM (2010) Towards an ecologically coherent network of well-managed Marine Protected Areas – Implementation report on the status and ecological coherence of the HELCOM BSPA network: Executive Summary., Baltic Sea Environment Proceedings No. 124A.

HELCOM (2012) Baltic Sea Environment Proceedings No. 130.

HELCOM (2016) Ecological coherence assessment of the Marine Protected Area network in the Baltic, Baltic Sea Environment Proceedings No. 148.

HELCOM (2018a) Sources and pathways of nutrients to the Baltic Sea, Baltic Sea Environment Proceedings No. 153.

HELCOM (2018b) State of the Baltic Sea – Second HELCOM holistic assessment 2011-2016, Baltic Sea Environment Proceedings 155.

Humborg, C., Geibel, M.C., Sun, X., McCrackin, M., Mörth, C.-M., Stranne, C., Jakobsson, M., Gustafsson, B., Sokolov, A., Norkko, A. and Norkko, J. (2019) High Emissions of Carbon Dioxide and Methane From the Coastal Baltic Sea at the End of a Summer Heat Wave. Frontiers in Marine Science 6, 493.

Hällfors, M.H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G.C. and Hellmann, J.J. (2016) Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecological Applications 26(4), 1154-1169.

Islam, M.S. and Tanaka, M. (2004) Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. Marine Pollution Bulletin 48(7-8), 624-649.

Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J. and Estes, J.A. (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530), 629-637.

Jackson, S.E. and Lundquist, C.J. (2016) Limitations of biophysical habitats as biodiversity surrogates in the Hauraki Gulf Marine Park. Pacific Conservation Biology 22(2), 159-172.

Janßen, H., Göke, C. and Luttmann, A. (2019) Knowledge integration in Marine Spatial Planning: A practitioners' view on decision support tools with special focus on Marxan. Ocean & Coastal Management 168, 130-138.

Jiménez-Valverde, A. and Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecologica 31(3), 361-369.

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P. and Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. Biological Invasions 13(12), 2785-2797.

Johnson, D.E., Froján, C.B., Turner, P.J., Weaver, P., Gunn, V., Dunn, D.C., Halpin, P., Bax, N.J. and Dunstan, P.K. (2018) Reviewing the EBSA process: improving on success. Marine Policy 88, 75-85.

Jokinen, S.A., Virtasalo, J.J., Jilbert, T., Kaiser, J., Dellwig, O., Arz, H.W., Hänninen, J., Arppe, L., Collander, M. and Saarinen, T. (2018) A 1500-year multiproxy record of coastal hypoxia from the northern Baltic Sea indicates unprecedented deoxygenation over the 20th century. Biogeosciences 15, 3975-4001.

Jones, K.R., Klein, C.J., Halpern, B.S., Venter, O., Grantham, H., Kuempel, C.D., Shumway, N., Friedlander, A.M., Possingham, H.P. and Watson, J.E.M. (2018) The Location and Protection Status of Earth’s Diminishing Marine Wilderness. Current Biology 28(15), 2506-2512.e2503.

Jones, P.J.S., Lieberknecht, L.M. and Qiu, W. (2016) Marine spatial planning in reality: Introduction to case studies and discussion of findings. Marine Policy 71(Supplement C), 256-264.

Jonsson, P.R., Granhag, L., Moschella, P.S., Åberg, P., Hawkins, S.J. and Thompson, R.C. (2006) Interactions between wave action and grazing control the distribution of intertidal macroalgae. Ecology 87(5), 1169-1178.

Jonsson, P.R., Kotta, J., Andersson, H.C., Herkül, K., Virtanen, E., Sandman, A.N. and Johannesson, K. (2018) High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former Fucus vesiculosus. Diversity and Distributions 24(7), 892-905.

Jonsson, P.R., Moksnes, P.-O., Corell, H., Bonsdorff, E. and Nilsson Jacobi, M. (2020) Ecological coherence of Marine Protected Areas: New tools applied to the Baltic Sea network. Aquatic Conservation: Marine and Freshwater Ecosystems n/a(n/a).

Jormalainen, V., Gagnon, K., Sjöroos, J. and Rothäusler, E. (2016) The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. Biological Invasions 18(5), 1409-1419.

Jouffray, J.-B., Blasiak, R., Norström, A.V., Österblom, H. and Nyström, M. (2020) The Blue Acceleration: The Trajectory of Human Expansion into the Ocean. One Earth 2(1), 43-54.

Kaikkonen, L., Venesjärvi, R., Nygård, H. and Kuikka, S. (2018) Assessing the impacts of seabed mineral extraction in the deep sea and coastal marine environments: Current methods and recommendations for environmental risk assessment. Marine Pollution Bulletin 135, 1183-1197.

Kallasvuo, M., Vanhatalo, J. and Veneranta, L. (2016) Modeling the spatial distribution of larval fish abundance provides essential information for management. Canadian Journal of Fisheries and Aquatic Sciences 74(5), 636-649.

Kareksela, S., Moilanen, A., Tuominen, S. and Kotiaho, J.S. (2013) Use of inverse spatial conservation prioritization to avoid biological diversity loss outside protected areas. Conserv Biol 27(6), 1294-1303.

Kaskela, A. and Rinne, H. (2018) Vedenalaisten Natura -luontotyyppien mallinnus Suomen merialueella, Geologian tutkimuskeskus.

Kaskela, A.M. and Kotilainen, A.T. (2017) Seabed geodiversity in a glaciated shelf area, the Baltic Sea. Geomorphology 295, 419-435.

Kaskela, A.M., Kotilainen, A.T., Al-Hamdani, Z., Leth, J.O. and Reker, J. (2012) Seabed geomorphic features in a glaciated shelf of the Baltic Sea. Estuarine, Coastal and Shelf Science 100, 150-161.

Kontula, T. and Raunio, A. (eds) (2019) Threatened Habitat Types in Finland 2018. Red List of Habitats – Results and Basis for Assessment. , Finnish Environment Institute and Ministry of the Environment, Helsinki.

Korpinen, S., Laamanen, M., Suomela, J., Paavilainen, P., Lahtinen, T. and Ekebom, J. (2018) Suomen meriympäristön tila 2018, Suomen ympäristökeskus, Suomen ympäristökeskus.

Korpinen, S., Meski, L., Andersen, J.H. and Laamanen, M. (2012) Human pressures and their potential impact on the Baltic Sea ecosystem. Ecological Indicators 15(1), 105-114.

Kotta, J., Nurkse, K., Puntila, R. and Ojaveer, H. (2016) Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby Neogobius melanostomus in a regional sea. Estuarine, Coastal and Shelf Science 169, 15-24.

Kotta, J., Vanhatalo, J., Jänes, H., Orav-Kotta, H., Rugiu, L., Jormalainen, V., Bobsien, I., Viitasalo, M., Virtanen, E., Sandman, A.N., Isaeus, M., Leidenberger, S., Jonsson, P.R. and Johannesson, K. (2019) Integrating experimental and distribution data to predict future species patterns. Scientific Reports 9(1), 1821.

Kuhn, T., Wegorzewski, A., Rühlemann, C. and Vink, A. (2017) Deep-Sea Mining, pp. 23-63, Springer.

Kukkala, A.S. and Moilanen, A. (2017) Ecosystem services and connectivity in spatial conservation prioritization. Landscape Ecology 32(1), 5-14.

Lappalainen, J., Kurvinen, L. and Kuismanen, L. (2020) Suomen ekologisesti merkittävät vedenalaiset meriluontoalueet (EMMA) – Finlands ekologiskt betydelsefulla marina undervattensmiljöer (EMMA). Autio, R. (ed), Suomen ympäristökeskus, Helsinki.

Lehtomäki, J. and Moilanen, A. (2013) Methods and workflow for spatial conservation prioritization using Zonation. Environmental Modelling & Software 47, 128-137.

Lehtomäki, J., Tomppo, E., Kuokkanen, P., Hanski, I. and Moilanen, A. (2009) Applying spatial conservation prioritization software and high-resolution GIS data to a national-scale study in forest conservation. Forest Ecology and Management 258(11), 2439-2449.

Lehtoranta, J. and Pitkänen, H. (2003) Binding of phosphate in sediment accumulation areas of the eastern Gulf of Finland, Baltic Sea. Hydrobiologia 492(1-3), 55-67.

Leppäranta, M. and Myrberg, K. (2009) Physical Oceanography of the Baltic Sea, Springer-Verlag, Berlin-Heidelberg-New York.

Lester, S., Stevens, J., Gentry, R., Kappel, C., Bell, T., Costello, C., Gaines, S., Kiefer, D., Maue, C. and Rensel, J. (2018) Marine spatial planning makes room for offshore aquaculture in crowded coastal waters. Nature communications 9(1), 1-13.

Lester, S.E. and Halpern, B.S. (2008) Biological responses in marine no-take reserves versus partially protected areas. Marine Ecology Progress Series 367, 49-56.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S. and Warner, R.R. (2009) Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384, 33-46.

Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28(3), 385-393.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. and Jackson, J.B. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312(5781), 1806-1809.

Martin, K.S. and Hall-Arber, M. (2008) The missing layer: Geo-technologies, communities, and implications for marine spatial planning. Marine Policy 32(5), 779-786.

Martínez, B., Arenas, F., Trilla, A., Viejo, R.M. and Carreño, F. (2015) Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. Global Change Biology 21(4), 1422-1433.

Meier, H.E.M., Andersson, H.C., Arheimer, B., Donnelly, C., Eilola, K., Gustafsson, B.G., Kotwicki, L., Neset, T.-S., Niiranen, S., Piwowarczyk, J., Savchuk, O.P., Schenk, F., Węsławski, J.M. and Zorita, E. (2014) Ensemble Modeling of the Baltic Sea Ecosystem to Provide Scenarios for Management. Ambio 43(1), 37-48.

Meier, H.E.M., Andersson, H.C., Eilola, K., Gustafsson, B.G., Kuznetsov, I., Müller-Karulis, B., Neumann, T. and Savchuk, O.P. (2011a) Hypoxia in future climates: A model ensemble study for the Baltic Sea. Geophysical Research Letters 38(24).

Meier, H.E.M., Edman, M.K., Eilola, K.J., Placke, M., Neumann, T., Andersson, H.C., Brunnabend, S.-E., Dieterich, C., Frauen, C., Friedland, R., Gröger, M., Gustafsson, B.G., Gustafsson, E., Isaev, A., Kniebusch, M., Kuznetsov, I., Müller-Karulis, B., Omstedt, A., Ryabchenko, V., Saraiva, S. and Savchuk, O.P. (2018) Assessment of Eutrophication Abatement Scenarios for the Baltic Sea by Multi-Model Ensemble Simulations. Frontiers in Marine Science 5, 440.

Meier, H.E.M., Eilola, K. and Almroth, E. (2011b) Climate-related changes in marine ecosystems simulated with a 3-dimensional coupled physical-biogeochemical model of the Baltic Sea. Climate Research 48(1).

Meier, H.E.M., Hordoir, R., Andersson, H.C., Dieterich, C., Eilola, K., Gustafsson, B.G., Hoglund, A. and Schimanke, S. (2012a) Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961-2099. Climate Dynamics 39(9-10), 2421-2441.

Meier, H.M., Müller-Karulis, B., Andersson, H.C., Dieterich, C., Eilola, K., Gustafsson, B.G., Höglund, A., Hordoir, R., Kuznetsov, I. and Neumann, T. (2012b) Impact of climate change on ecological quality indicators and biogeochemical fluxes in the Baltic Sea: a multi-model ensemble study. Ambio 41(6), 558-573.

Mitchell, P.J., Monk, J. and Laurenson, L. (2017) Sensitivity of fine-scale species distribution models to locational uncertainty in occurrence data across multiple sample sizes. Methods in Ecology and Evolution 8(1), 12-21.

Moilanen, A. (2007) Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. Biological Conservation 134(4), 571-579.

Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B. and Thomas, C.D. (2005) Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B-Biological Sciences 272(1575), 1885-1891.

Moilanen, A. and Kujala, H. (2014) Zonation spatial conservation planning framework and software v. 4.0, User Manual. Helsinki, Finland: University of Helsinki.

Moilanen, A., Kujala, H. and Mikkonen, N. (2020) A practical method for evaluating spatial biodiversity offset scenarios based on spatial conservation prioritization outputs.

Methods in Ecology and Evolution 11, 794-803.
Moksnes, P.O., Gullström, M., Tryman, K. and Baden, S. (2008) Trophic cascades in a temperate seagrass community. Oikos 117(5), 763-777.
Molinos, J.G., Halpern, B.S., Schoeman, D.S., Brown, C.J., Kiessling, W., Moore, P.J., Pandolfi, J.M., Poloczanska, E.S., Richardson, A.J. and Burrows, M.T. (2016) Climate velocity and the future global redistribution of marine biodiversity. Nature Climate Change 6(1), 83-88.
Morán-Ordóñez, A., Lahoz-Monfort, J.J., Elith, J. and Wintle, B.A. (2017) Evaluating 318 continental-scale species distribution models over a 60-year prediction horizon: what factors influence the reliability of predictions? Global Ecology and Biogeography 26(3), 371-384.
Moss, B. (2008) The Water Framework Directive: total environment or political compromise? Science of The Total Environment 400(1-3), 32-41.
MSFD (2012) Contribution of the Marine Strategy Framework Directive (2008/56/EC) to the implementation of existing obligations, commitments and initiatives of the Member States or the EU at EU or international level in the sphere of environmental protection in marine waters.
MSPD (2014) Maritime spatial planning for the sustainable development and growth of Europe's maritime areas.
Neumann, T. (2010) Climate-change effects on the Baltic Sea ecosystem: A model study. Journal of Marine Systems 81(3), 213-224.
Nieminen, E., Ahtiainen, H., Lagerkvist, C.-J. and Oinonen, S. (2019) The economic benefits of achieving Good Environmental Status in the Finnish marine waters of the Baltic Sea. Marine Policy 99, 181-189.
Nilsson, J., Engkvist, R. and Persson, L.-E. (2004) Long-term decline and recent recovery of Fucus populations along the rocky shores of southeast Sweden, Baltic Sea. Aquatic Ecology 38(4), 587-598.
Norberg, A., Abrego, N., Blanchet, F.G., Adler, F.R., Anderson, B.J., Anttila, J., Araújo, M.B., Dallas, T., Dunson, D., Elith, J., Foster, S.D., Fox, R., Franklin, J., Godsoe, W., Guisan, A., O'Hara, B., Hill, N.A., Holt, R.D., Hui, F.K.C., Husby, M., Kålås, J.A., Lehikoinen, A., Luoto, M., Mod, H.K., Newell, G., Renner, I., Roslin, T., Soininen, J., Thuiller, W., Vanhatalo, J., Warton, D., White, M., Zimmermann, N.E., Gravel, D. and Ovaskainen, O. (2019) A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. Ecological Monographs 89(3), e01370.
Norkko, J., Gammal, J., Hewitt, J.E., Josefson, A.B., Carstensen, J. and Norkko, A. (2015) Seafloor Ecosystem Function Relationships: In Situ Patterns of Change Across Gradients of Increasing Hypoxic Stress. Ecosystems 18(8), 1424-1439.
Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B.G., Bonsdorff, E., Slomp, C.P., Carstensen, J. and Conley, D.J. (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. Global Change Biology 18(2), 422-434.
Nyström, M., Jouffray, J.B., Norström, A.V., Crona, B., Søgaard Jørgensen, P., Carpenter, S.R., Bodin, Ö., Galaz, V. and Folke, C. (2019) Anatomy and resilience of the global production ecosystem. Nature 575(7781), 98-108.
Oh, B.Z., Sequeira, A.M., Meekan, M.G., Ruppert, J.L. and Meeuwig, J.J. (2017) Predicting occurrence of juvenile shark habitat to improve conservation planning. Conservation Biology 31(3), 635-645.
Ojaveer, H., Jaanus, A., MacKenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L. and Zaiko, A. (2010) Status of biodiversity in the Baltic Sea. PLOS ONE 5(9), e12467.
Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T. and Abrego, N. (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20(5), 561-576.
Peukert, A., Schoening, T., Alevizos, E., Köser, K., Kwasnitschka, T. and Greinert, J. (2018) Understanding Mn-nodule distribution and evaluation of related deep-sea mining impacts using AUV-based hydroacoustic and optical data. Biogeosciences 15(8), 2525-2549.
Pınarbaşı, K., Galparsoro, I., Borja, A., Stelzenmüller, V., Ehler, C. and Gimpel, A. (2017) Decision support tools in marine spatial planning: Present applications, gaps and future perspectives. Marine Policy 83, 83-91.
Pittman, S.J. (2017) Seascape ecology, John Wiley & Sons.
Poloczanska, E.S., Burrows, M.T., Brown, C.J., García Molinos, J., Halpern, B.S., Hoegh-

Guldberg, O., Kappel, C.V., Moore, P.J., Richardson, A.J. and Schoeman, D.S. (2016) Responses of marine organisms to climate change across oceans. Frontiers in Marine Science 3, 62.

Puttonen, I., Kohonen, T. and Mattila, J. (2016) Factors controlling phosphorus release from sediments in coastal archipelago areas. Marine Pollution Bulletin 108(1-2), 77-86.

Puttonen, I., Mattila, J., Jonsson, P., Karlsson, O.M., Kohonen, T., Kotilainen, A., Lukkari, K., Malmaeus, J.M. and Rydin, E. (2014) Distribution and estimated release of sediment phosphorus in the northern Baltic Sea archipelagos. Estuarine, Coastal and Shelf Science 145, 9-21.

Raateoja, M. and Setälä, O. (2016) The Gulf of Finland Assessment, Finnish Environment Institute.

Rabalais, N.N., Diaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D. and Zhang, J. (2010) Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences 7(2), 585-619.

Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R. and Van Dover, C.L. (2011) Man and the Last Great Wilderness: Human Impact on the Deep Sea. PLOS ONE 6(8), e22588.

Reusch, T.B.H., Dierking, J., Andersson, H.C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., Hasler, B., Hinsby, K., Hyytiäinen, K., Johannesson, K., Jomaa, S., Jormalainen, V., Kuosa, H., Kurland, S., Laikre, L., MacKenzie, B.R., Margonski, P., Melzner, F., Oesterwind, D., Ojaveer, H., Refsgaard, J.C., Sandström, A., Schwarz, G., Tonderski, K., Winder, M. and Zandersen, M. (2018) The Baltic Sea as a time machine for the future coastal ocean. Science Advances 4(5).

Rinne, H., Björklund, C., Hämäläinen, J., Häggblom, M. and Salovius-Laurén, S. (2019) Rapport nr 153: Mapping Marine Natura 2000 habitats in Åland Final report.

Rinne, H., Kaskela, A., Downie, A.L., Tolvanen, H., von Numers, M. and Mattila, J. (2014) Predicting the occurrence of rocky reefs in a heterogeneous archipelago area with limited data. Estuarine Coastal and Shelf Science 138, 90-100.

Rinne, H. and Salovius-Laurén, S. (2019) The status of brown macroalgae Fucus spp. and its relation to environmental variation in the Finnish marine area, northern Baltic Sea. Ambio 49(1), 118-129.

Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P. and Richardson, A.J. (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global Ecology and Biogeography 20(6), 789-802.

Robinson, N.M., Nelson, W.A., Costello, M.J., Sutherland, J.E. and Lundquist, C.J. (2017) A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice. Frontiers in Marine Science 4, 421.

Rocha, J., Yletyinen, J., Biggs, R., Blenckner, T. and Peterson, G. (2015) Marine regime shifts: drivers and impacts on ecosystems services. Philosophical Transactions of the Royal Society B: Biological Sciences 370(1659), 20130273.

Rouillard, J., Lago, M., Abhold, K., Röschel, L., Kafyeke, T., Mattheiß, V. and Klimmek, H. (2018) Protecting aquatic biodiversity in Europe: How much do EU environmental policies support ecosystem-based management? Ambio 47(1), 15-24.

Ruuskanen, A. (2016) The occurrence and monitoring of macroalgae in the coastal waters of Uusimaa. The description of national macrophyte monitoring and application in Uusimaa 1993–016. .

Sagerman, J., Hansen, J.P. and Wikström, S.A. (2020) Effects of boat traffic and mooring infrastructure on aquatic vegetation: A systematic review and meta-analysis. Ambio 49(2), 517-530.

Santangeli, A., Butchart, S.H., Pogson, M., Hastings, A., Smith, P., Girardello, M. and Moilanen, A. (2018) Mapping the global potential exposure of soaring birds to terrestrial wind energy expansion. Ornis Fennica 95(1), 1-14.

Saraiva, S., Markus Meier, H.E., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R. and Eilola, K. (2019) Baltic Sea ecosystem response to various nutrient load scenarios in present and future climates. Climate Dynamics 52(5), 3369-3387.

Savchuk, O.P. (2000) Studies of the assimilation capacity and effects of nutrient load reductions in the eastern Gulf of Finland with a biogeochemical model. Boreal Environment Research 5(2), 147-163.

Sharp, R., Tallis, H., Ricketts, T., Guerry, A., Wood, S., Chaplin-Kramer, R., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C., Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J., Marsik, M., Bernhardt, J., Griffin, R., Glowinski, K., Chaumont, N., Perelman, A., Lacayo, M., Mandle, L., Hamel, P., Vogl, A.L., Rogers, L., Bierbower, W., Denu, D. and Douglass, J. (2018) InVEST 3.6.0 User's Guide. The Natural Capital Project, Stanford University, University of Minnesota, The Nature Conservancy, and World Wildlife Fund.

Snoeijs-Leijonmalm, P., Schubert, H. and Radziejewska, T. (2017) Biological oceanography of the Baltic Sea, Springer Science & Business Media.

Stelzenmüller, V., Lee, J., South, A., Foden, J. and Rogers, S.I. (2013) Practical tools to support marine spatial planning: a review and some prototype tools. Marine Policy 38, 214-227.

Stevens, T. and Connolly, R.M. (2004) Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. Biological Conservation 119(3), 351-362.

Sunday, J.M., Bates, A.E. and Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. Nature Climate Change 2(9), 686-690.

Sundblad, G., Bergstrom, U. and Sandstrom, A. (2011) Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. Journal of Applied Ecology 48(1), 112-120.

Sundblad, G. and Bergström, U. (2014) Shoreline development and degradation of coastal fish reproduction habitats. Ambio 43(8), 1020-1028.

Takolander, A., Cabeza, M. and Leskinen, E. (2017a) Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review. Journal of Sea Research 123, 16-29.

Takolander, A., Leskinen, E. and Cabeza, M. (2017b) Synergistic effects of extreme temperature and low salinity on foundational macroalga Fucus vesiculosus in the northern Baltic Sea. Journal of Experimental Marine Biology and Ecology 495, 110-118.

Thomson, J.R., Moilanen, A., Vesk, P., Bennett, A.F. and Nally, R.M. (2009) Where and when to revegetate: a quantitative method for scheduling landscape reconstruction. Ecological Applications 19(4), 817-828.

Torn, K., Krause-Jensen, D. and Martin, G. (2006) Present and past depth distribution of bladderwrack (Fucus vesiculosus) in the Baltic Sea. Aquatic Botany 84(1), 53-62.

Vahtera, E., Conley, D.J., Gustafsson, B.G., Kuosa, H., Pitkanen, H., Savchuk, O.P., Tamminen, T., Viitasalo, M., Voss, M., Wasmund, N. and Wulff, F. (2007) Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. Ambio 36(2-3), 186-194.

Vahteri, P. and Vuorinen, I. (2016) Continued decline of the bladderwrack, Fucus vesiculosus, in the Archipelago Sea, northern Baltic proper. Boreal Environment Research 21, 373-386.

Walve, J., Sandberg, M., Larsson, U. and Lannergren, C. (2018) A Baltic Sea estuary as a phosphorus source and sink after drastic load reduction: seasonal and long-term mass balances for the Stockholm inner archipelago for 1968-2015. Biogeosciences 15(9), 3003-3025.

van Denderen, P.D., Bolam, S.G., Friedland, R., Hiddink, J.G., Norén, K., Rijnsdorp, A.D., Sköld, M., Törnroos, A., Virtanen, E.A. and Valanko, S. (2019) Evaluating impacts of bottom trawling and hypoxia on benthic communities at the local, habitat, and regional scale using a modelling approach. ICES Journal of Marine Science 77(1), 278-289.

Vaquer-Sunyer, R. and Duarte, C.M. (2008) Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences of the United States of America 105(40), 15452-15457.

Weatherdon, L.V., Ota, Y., Jones, M.C., Close, D.A. and Cheung, W.W. (2016) Projected scenarios for coastal First Nations' fisheries catch potential under climate change: management challenges and opportunities. PLOS ONE 11(1).

Weinert, M., Mathis, M., Kroencke, I., Neumann, H., Pohlmann, T. and Reiss, H. (2016) Modelling climate change effects on benthos: Distributional shifts in the North Sea from 2001 to 2099. Estuarine, Coastal and Shelf Science 175, 157-168.

Verbruggen, H., Tyberghein, L., Belton, G.S., Mineur, F., Jueterbock, A., Hoarau, G., Gurgel, C.F.D. and De Clerck, O. (2013) Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLOS ONE 8(6), e68337.

Verhagen, W., Kukkala, A.S., Moilanen, A., van Teeffelen, A.J.A. and Verburg, P.H. (2017) Use of demand for and spatial flow of ecosystem services to identify priority areas. Conservation Biology 31(4), 860-871.

Viitasalo, M., Kostamo, K., Hallanaro, E.-L., Viljanmaa, W., Kiviluoto, S., Ekebom, J. and Blankett, P. (eds) (2017) Meren aarteet, Gaudeamus.

Willis, S., Foden, W., Baker, D., Belle, E., Burgess, N., Carr, J., Doswald, N., Garcia, R., Hartley, A. and Hof, C. (2015) Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. Biological Conservation 190, 167-178.

Villnäs, A., Norkko, J., Hietanen, S., Josefson, A.B., Lukkari, K. and Norkko, A. (2013) The role of recurrent disturbances for ecosystem multifunctionality. Ecology 94(10), 2275-2287.

Villnäs, A., Norkko, J., Lukkari, K., Hewitt, J. and Norkko, A. (2012) Consequences of Increasing Hypoxic Disturbance on Benthic Communities and Ecosystem Functioning. PLOS ONE 7(10), e44920.

Virtanen, E.A., Moilanen, A. and Viitasalo, M. (2020) Marine connectivity in spatial conservation planning: analogues from the terrestrial realm. Landscape Ecology 35(5), 1021-1034.

Virtasalo, J.J., Kohonen, T., Vuorinen, I. and Huttula, T. (2005) Sea bottom anoxia in the Archipelago Sea, northern Baltic Sea—Implications for phosphorus remineralization at the sediment surface. Marine Geology 224(1), 103-122.

Worm, B., Barbier, E., Beaumont, N., Duffy, J., Folke, C., Halpern, B., Jackson, J., Lotze, H., Micheli, F., R Palumbi, S., Sala, E., Selkoe, K., Stachowicz, J. and Watson, R. (2006) Impacts of Biodiversity Loss on Ocean Ecosystem Services. 314(5800), 787-790.

Voulvoulis, N., Arpon, K.D. and Giakoumis, T. (2017) The EU Water Framework Directive: From great expectations to problems with implementation. Science of The Total Environment 575, 358-366.

Vuorinen, I., Hänninen, J., Rajasilta, M., Laine, P., Eklund, J., Montesino-Pouzols, F., Corona, F., Junker, K., Meier, H.M. and Dippner, J.W. (2015) Scenario simulations of future salinity and ecological consequences in the Baltic Sea and adjacent North Sea areas–implications for environmental monitoring. Ecological Indicators 50, 196-205.

Wåhlström, I., Höglund, A., Almroth-Rosell, E., MacKenzie, B.R., Gröger, M., Eilola, K., Plikshs, M. and Andersson, H.C. (2020) Combined climate change and nutrient load impacts on future habitats and eutrophication indicators in a eutrophic coastal sea. Limnology and Oceanography 65, 2170-2187.

Yli-Hemminki, P., Sara-Aho, T., Jørgensen, K.S. and Lehtoranta, J. (2016) Iron–manganese concretions contribute to benthic release of phosphorus and arsenic in anoxic conditions in the Baltic Sea. Journal of Soils and Sediments 16(8), 2138-2152.

Zhamoida, V., Grigoriev, A., Gruzdov, K. and Ryabchuk, D. (2007) The influence of ferromanganese concretions-forming processes in the eastern Gulf of Finland on the marine environment. Geological Survey of Finland Special Papers 45, 21-32.

Zhamoida, V., Grigoriev, A., Ryabchuk, D., Evdokimenko, A., Kotilainen, A.T., Vallius, H. and Kaskela, A.M. (2017) Ferromanganese concretions of the eastern Gulf of Finland – Environmental role and effects of submarine mining. Journal of Marine Systems 172, 178-187.

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R. and Folke, C. (2007) Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems 10(6), 877-889.